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The Canadian Entomologist

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The Canadian Entomologist

Vol. XCI Ottawa, Canada, December 1959 No. 12

A New Family of Trichoptera from Asia[1]

By Glenn B. Wiggins

Department of Invertebrates, Royal Ontario Museum
Toronto 5, Canada

In 1906 Nathan Banks described a species, *Phryganea latipennis*, based on a single male specimen which he had received in a collection of caddisflies from Japan. Assignment of this species to the family Phryganeidae has always seemed the logical course because the adults possessed the typical phryganeid characters of ocelli, four-segmented maxilary palpi in the male, and five-segmented palpi in the female, with a tibial spur count of 2, 4, 4. That the species was a phryganeid has never been questioned in the past, and in a preliminary revision of the family Phryganeidae, Martynov (1924) created a new genus *Phryganopsis* for the single species *latipennis* Banks. A second species, *cornuta*, from Burma, was added to the genus by Kimmins (1950). It was not until 1951 that the larva and case of *P. latipennis* were figured and briefly described by Tsuda. This was the first published information on the immature stages of the genus, and the structures of the pupa have still not been made known.

Unfortunately, the name *Phryganopsis* Martynov, 1924, (type, by monotypy, *Phryganea latipennis* Banks, 1906) is preoccupied by *Phryganopsis* Felder, 1874, (Reise der Novara, Zool. 2, Abt. 2, Lep. Het., Explan. pls. 75-107, 8; type, by monotypy, *Phryganopsis sordida* Felder, *op. cit.*, pl. 106, fig. 30), a name applied to a genus of the lepidopterous family Lithosiidae. I am informed by Dr. E. G. Munroe that *Phryganopsis* Felder is a valid name for this genus which contains nearly thirty species. Professor Martynov died many years ago, and therefore as the first function of this paper I am proposing the new generic name *Phryganopsyche*, with type species *Phryganea latipennis* Banks, 1906, to replace the preoccupied name *Phryganopsis* Martynov.

The second, and principal, function of this paper is to present evidence to show that species of this genus *Phryganopsyche* possess a number of characters which are unique and discordant among the known species of the Phryganeidae. It is my interpretation of the evidence that this genus represents a phyletic line in which there are combined certain characters, which also appear in a number of other families, such as the Limnephilidae, the Brachycentridae, and the Lepidostomatidae, as well as the Phryganeidae, along with certain other characters which are unusual, if not unique, in the whole order Trichoptera. My conclusion from this evidence is that at the present time the ends of both practical taxonomy and theoretical phylogeny can best be served by the removal of the genus *Phryganopsyche* from the family Phryganeidae. Owing to the fact that no single family now recognized within the Trichoptera encompasses the set of characters possessed by the genus *Phryganopsyche*, I can see no alternative to the creation of a new family for this genus. Accordingly, I am proposing the name Phryganopsychidae for this family. Following is the evidence upon which this action is based.

[1]This paper is based on one section of a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy in the University of Toronto, 1958.

Evidence from the Larva

1. The terga of both the prothorax and mesothorax of the larva of *Phryganopsyche latipennis* are each covered with a pair of dark brown sclerotized plates (Figs. 1, 3). This is also true of larvae of many other families, including the Lepidostomatidae and Limnephilidae, but it is not true of any known phryganeid larvae. In the Phryganeidae the pronotum alone bears a pair of sclerotized plates, the mesonotum and metanotum usually being membranous (Fig. 9), although an exception to this occurs in the phryganeid genera *Oligostomis* and *Holostomis* in which the mesonotum bears a small median area which is weakly sclerotized.

2. The head of the larva of *P. latipennis* (Fig. 3) is uniform dark brown. Uniform dark brown heads occur in larvae of many other families, but not in any known larvae of the Phryganeidae. In phryganeid larvae the head (Fig. 9) has a conspicuous colour pattern of dark brown bands separated by lighter, yellowish areas.

3. The apical portion of the labium of *P. latipennis* is elongate and rather narrow, and bears a pair of elongate subparallel sclerites on its ventral surface. The labial palpi originate dorsolaterally, each with a very long, terminal segment (Figs. 4, 8). In larvae of the Phryganeidae, the apical portion of the labium is short and thick, and the elongate sclerites on its ventral surface are broadly convergent. The labial palpi originate laterally, and the terminal segment is shorter than in *P. latipennis* (Figs. 10, 11).

4. In the maxilla of *P. latipennis* (Fig. 4) the apicomesal lobe is thick, rounded and hairy, somewhat resembling the maxillary lobe of the Lepidostomatidae, and to some extent, the Goeridae. The basal portion, which also supports the segmented maxillary palp, is sclerotized laterally, but mesally has an oval membranous area from which a patch of long hairs originates. In the maxillae of phryganeid larvae (Fig. 10) the apicomesal lobe is slender and finger-like, and is not hairy. The basal portion, which also supports the segmented maxillary palp, has quite a different arrangement of sclerotized areas and does not bear long hairs.

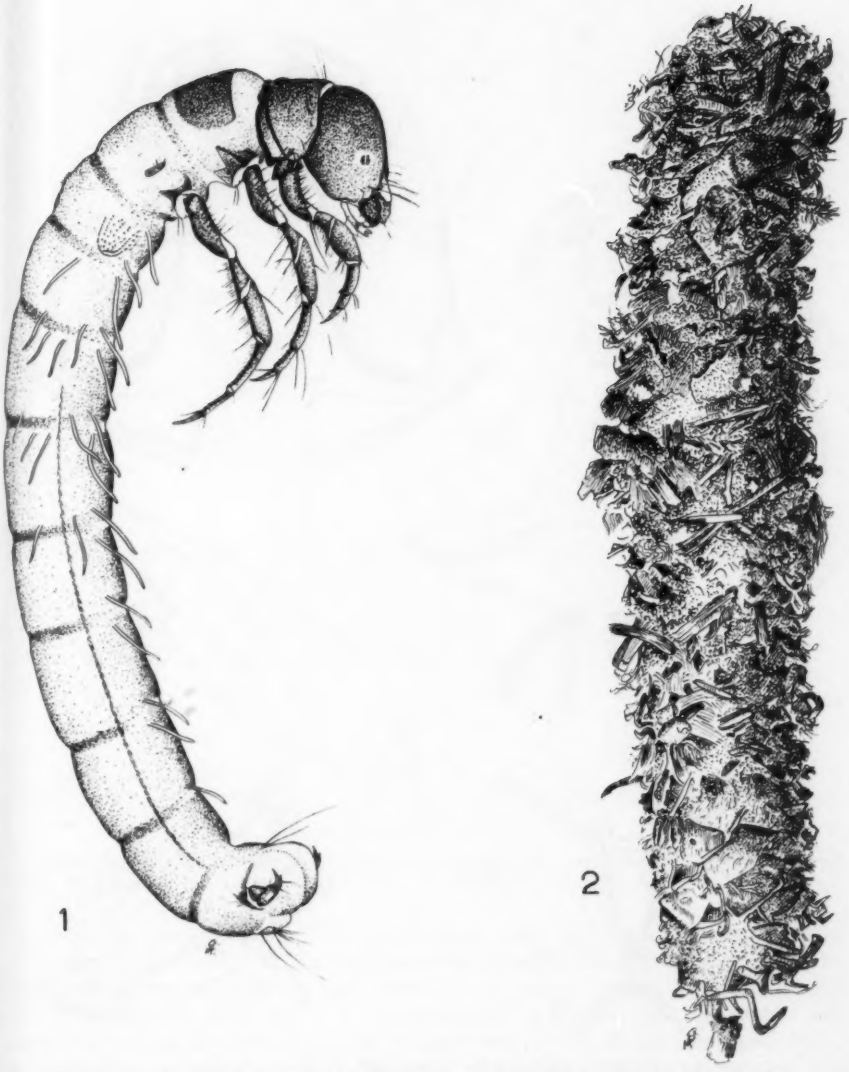
5. On the membranous metanotum of the larva of *P. latipennis*, seta 3 (*sensu* Ross, 1956) is represented by several setae arising from a thin sclerotized bar (Fig. 3), much as in the Lepidostomatidae. In phryganeid larvae seta 3 on both the membranous mesonotum and metanotum is represented by a cluster of setae arising from a rounded, sclerotized button (Fig. 9).

6. The large lateral sclerite at the base of each anal leg in the larva of *P. latipennis* (Fig. 1) bears a patch of dark hairs at the point of articulation of the terminal claw. In phryganeid larvae this patch of hairs is not present.

7. The larval case of *P. latipennis* (Fig. 2) is very flimsy and is unevenly constructed of assorted bits of detritus fastened together irregularly, somewhat as in certain limnephilids. In phryganeid larvae the case is much more rigid and is constructed of plant pieces fashioned into a fairly regular tube with a smooth outline.

Evidence from the Adult

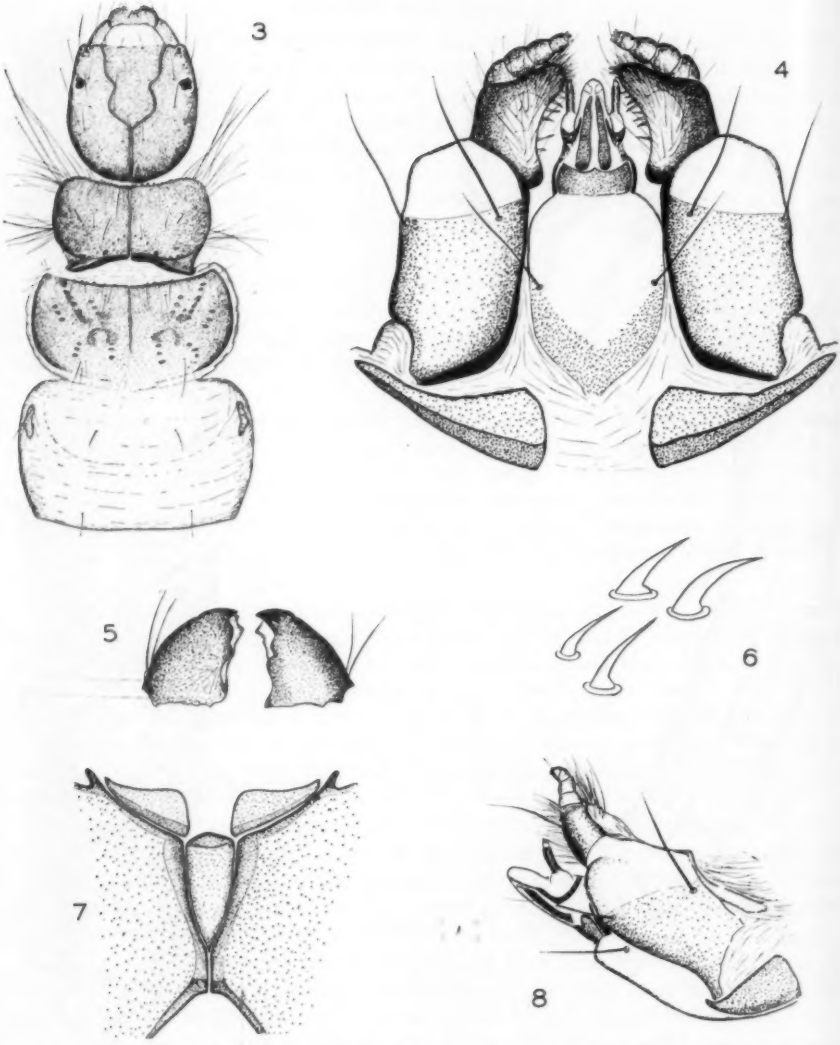
8. The head of *Phryganopsyche* adults bears three separate triangular warts immediately behind the median ocellus (Fig. 14b). Among the ocellate groups which construct tubular cases the closest similarity to this arrangement of head warts that is known to me is in the kitagamiid genus *Limnocentropus*, where, although the larger anteromedian wart is divided into two, the posterolateral pair



Figs. 1, 2. 1, Larva of *Phryganopsyche latipennis;* 2, Larval case of *Phryganopsyche latipennis.*

is well developed as in *Phryganopsyche.* In the Phryganeidae there is only a pair of warts in this position. (Fig. 12b).

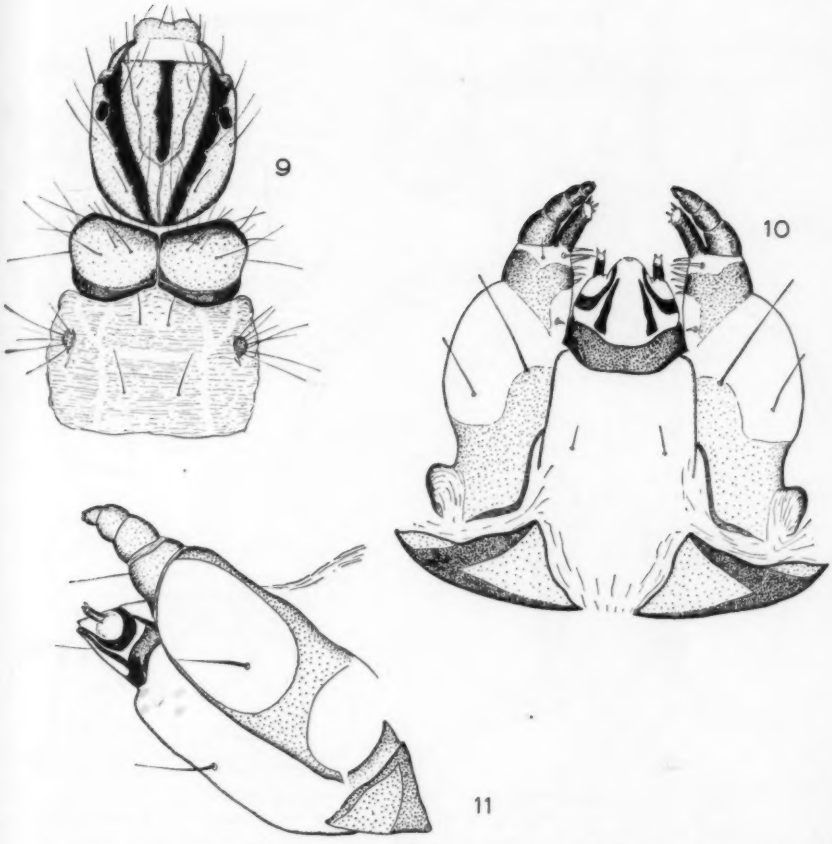
9. The labrum in *Phryganopsyche* adults (Fig. 14a) is rather broad in relation to its length, the length being somewhat less than twice the width, and rather similar in shape to that of the kitagamiid genus *Limnocentropus.* In the Phryganeidae the labrum (Fig. 12a) is long and narrow, the length being at least twice the width.



Figs. 3-8., Larva of *Phryganopsyche latipennis*. 3, Head and thorax, dorsal view; 4, Maxillae and labium, ventral view; 5, Mandibles, dorsal view; 6, A few of the bristles on the lateral humps of the first abdominal segment; 7, Portion of the head capsule showing genae separated by the gular sclerite, ventral view, anterior edge uppermost; 8, Maxilla and labium, lateral view.

10. In *Phryganopsyche* adults the two anterior tentorial pits (Fig. 14a) are situated in the ventrolateral corners of the frontoclypeus. These pits occur in about the same position in a number of other families such as the Rhyacophilidae, Brachycentridae, and Lepidostomatidae. In the Phryganeidae the anterior tentorial pits are situated in about the middle of the frontoclypeus (Fig. 12a).

11. The segments of the antennae in *Phryganopsyche* adults are simple and

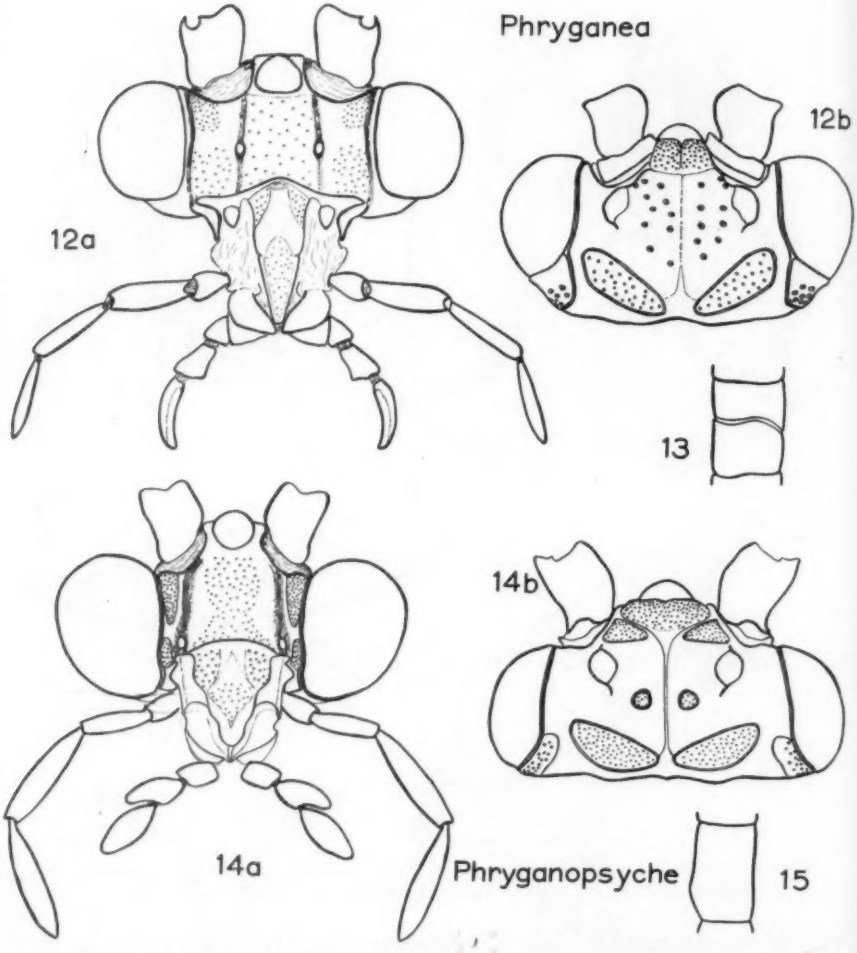


Figs. 9-11, Larva of *Phryganea cinerea*. 9, Head and first two thoracic segments, dorsal view; 10, Maxillae and labium, ventral view; 11, Maxilla and labium, lateral view.

without any conspicuous surface depressions (Fig. 15). This applies to most other families, as well. In the Phryganeidae, however, all of the segments of the antennae, except a few at the apex, have a deep curved groove extending around the circumference (Fig. 13). A somewhat similar groove, although nearer the distal end of the segment, occurs in at least some species of the Limnephilidae.

12. In the fore wing of *Phryganopsyche* (Fig. 16) the anterior margin of the discoidal cell, R_{2+3}, is sharply humped, and the separation of R_2 from R_3, and of R_4 from R_5, lies at about the same level. A somewhat similar arrangement of these veins occurs in such families as the Limnephilidae and Brachycentridae. In the Phryganeidae, however, the anterior margin of the discoidal cell is fairly straight and the point of separation of R_2 from R_3 is some distance basad of the point of separation of R_4 from R_5 (Fig. 17).

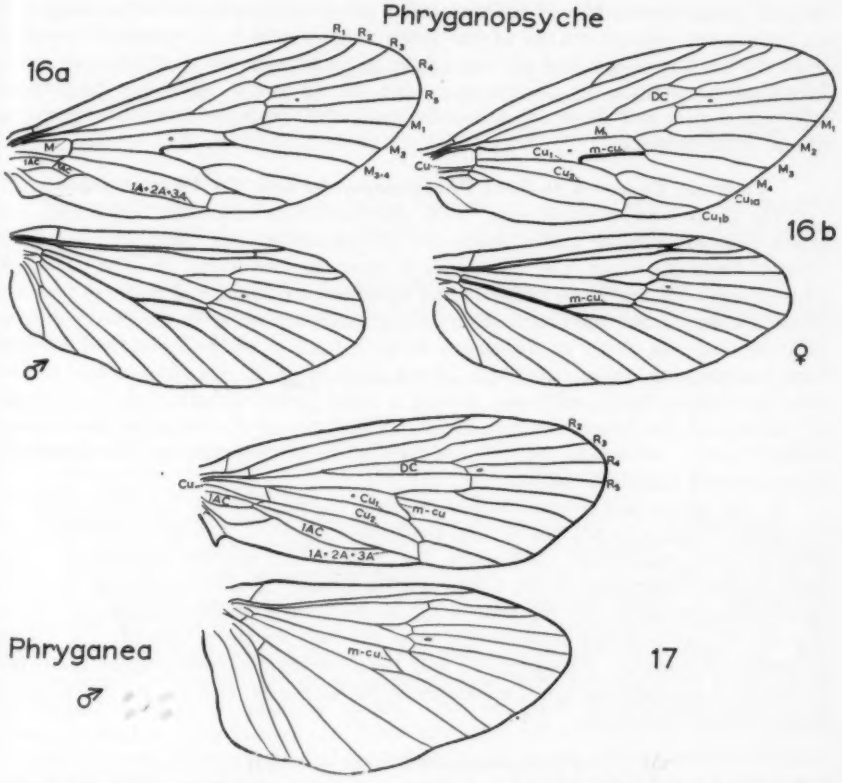
13. In the fore wing of *Phryganopsyche* (Fig. 16) the base of Cu_1 meets a short spur from M, and this spur, lining up with a sharp angle in Cu_1 following its separation from Cu_2, makes a straight connection between M and Cu_2 which looks like a crossvein with Cu_1 joining it in the middle. This is an unusual



Figs. 12-15. 12, Head of adult male of *Phryganea cinerea*, 12a face view, 12b dorsal view; 13, segment of antenna of *Phryganea cinerea;* 14, Head of adult male of *Phryganopsyche latipennis,* 14a face view, 14b dorsal view; 15, segment of antenna of *Phryganopsyche latipennis.*

venational feature in the Trichoptera, and I do not know of any other families in which it occurs in just this way. Dr. H. H. Ross has pointed out to me, however, that the angulate base of Cu_1, along with the spur from M, together constituting the arculus, are found in some species of the Hydrobiosinae, a subfamily of the Rhyacophilidae, (Ross, 1951, Figs. 5, 6). The two components of the arculus in these instances remain angulate, however, and are not aligned to form an apparent straight crossvein as in *Phryganopsyche.* In the Phryganeidae the base of Cu_1 separates from Cu_2 at a sharp angle, and then usually meets the base of M in a single point (Fig. 17), although sometimes there is a very short spur joining M with the base of Cu_1 (Wiggins, 1956, Fig. 2b).

14. Crossvein m-cu in the fore wing of *Phryganopsyche* (Fig. 16) is very long



Figs. 16, 17. 16, Wings of *Phryganopsyche latipennis*, 16a male, 16b female; 17, Wings of male of *Phryganea grandis*. (DC- discoidal cell; 1AC - first anal cell).

and thick, and with its axis parallel to the long axis of the wing, extends from a point on M_{3+4} to a point on Cu_1 that is some distance basad of the separation of Cu_{1a} and Cu_{1b}. This is again an unusual venational feature in the Trichoptera and I do not know of any other families in which it occurs, but it is not found in any known species of the Phryganeidae. In the Phryganeidae crossvein m-cu in the fore wing is not thickened, and extends, with its axis at right angles to the long axis of the wing, from a point at or near the first separation of the terminal branches of M to a point at or near the separation of Cu_{1a} and Cu_{1b} (Fig. 17). A similar comparison can be made for the position of m-cu in the hind wing of these two groups.

15. In the forewing of *Phryganopsyche* (Fig. 16) the length of the single united anal vein, 1A + 2A + 3A, is approximately twice that of the two parts of the first anal cell combined. This is a fairly typical feature of such families as the Limnephilidae, where the length of the first anal cell and vein 1A + 2A + 3A may sometimes be approximately equal, and the Brachycentridae. In the Phryganeidae, however, the first anal cell is considerably longer, with the result that vein 1A + 2A + 3A is only one-quarter to one-third the length of the first anal cell (Fig. 17).

16. In the female genitalia of *Phryganopsyche* (Figs. 19, 22) a membranous band

extends across the middle of the subgenital plate, and there is a rather long lobe on each posterolateral corner of the ninth tergum which is separated ventrally from the median sclerotized portion of the ninth tergum by a membranous area. In all known females of the Phryganeidae the subgenital plate is a continuous sclerotized plate and there are no membranous areas between sclerotized portions of the ninth tergum.

Features Common to both *Phryganopsyche* and the Phryganeidae

Up to this point there have been discussed only characters in which the genus *Phryganopsyche* differs from the Phryganeidae, but there are, however, certain features which the two groups have in common. In the larva of *Phryganopsyche latipennis* (Fig. 3) the antennae are short and peg-like and are situated close to the anterior margin of the head capsule as in the Phryganeidae (Fig. 9), and not closer to the eye as in such families as the Limnephilidae and Lepidostomatidae. The mandibles of the larva (Fig. 5) are also similar to the usual phryganeid type, each one lacking a mesal brush of hairs, but with a pair of bristles on the posterolateral corner. The larva of *P. latipennis* has a prosternal horn, a structure that also occurs in the Phryganeidae, Limnephilidae, Goeridae and Lepidostomatidae.

In the adults of *Phryganopsyche* the four segments in the maxillary palpi of the male, with five in the female, and the tibial spurs of 2, 4, 4 in both sexes, have already been mentioned, and these are typical phryganeid characters. The warts on the mesonotum of the adults of *Phryganopsyche* are also similar to those of the Phryganeidae. In the fore wing of the female of *Phryganopsyche* veins M_3 and M_4 are separate, while in the male the two are fused into M_{3+4}. This is similar to both the Phryganeidae and Brachycentridae, and distinct from the Goeridae, Limnephilidae and Lepidostomatidae where M_3 and M_4 are fused in the fore wings of both sexes.

Phryganopsychidae, new family

Adults. Maxillary palpi four-segmented in the male, five-segmented in the female. Ocelli present. Dorsum of the head with a single median wart behind the median ocellus, followed immediately by a smaller triangular wart at each posterolateral corner. Anterior tentorial pits situated far in the ventrolateral corners of the frontoclypeus. Fore wing with the anterior margin of the discoidal cell strongly curved; the separation of R_2 and R_3 approximately in line with the separation of R_4 and R_5; base of Cu_1 sharply angulate and aligned with a spur from M to form an apparent straight crossvein between M and Cu_2; length of vein 1A + 2A + 3A approximately twice the length of the first anal cell. Both fore and hind wings with crossvein m-cu thick, parallel to the long axis of the wing, and approximately as long as the discoidal cell. Tibial spurs 2, 4, 4.

Pupae. Undescribed.

Larvae. Antennae short and peg-like, situated close to the anterior margin of the head capsule. Pronotum and mesonotum each with a pair of heavily sclerotized plates; metanotum entirely membranous; pronotum crossed by a transverse furrow or fold just in front of the posterior margin; prosternal horn present. Larval case cylindrical, loosely constructed of plant fragments, occasionally with sand grains or other mineral materials added.

Type genus: *Phryganopsyche* Wiggins.

This family is, of course, one of the group in which the adults possess ocelli and the larvae construct a tubular, portable case, i.e. the limnephilid line of Ross (1956). As indicated previously, the Phryganopsychidae combine a number of

the characters that also occur in the other families of this line, along with some that are unique.

Phryganopsyche, new name

Phryganopsis Martynov, 1924, p. 211; type by monotypy, *Phryganea latipennis* Banks, 1906. Preoccupied by *Phryganopsis* Felder, 1874, Reise der Novara, Zool. 2, Abt. 2, Lep. Het., Explan. Pls. 75-107, 8; type by monotypy, *Phryganopsis sordida* Felder, *op. cit*, Pl. 106, Fig. 30.

Phryganopsis Kimmins, 1950, p. 697.

Since there is only a single genus recognized in this family at the present time, the diagnostic characters of the genus are the same as those outlined above for the family.

Type species, by present designation: *Phryganea latipennis* Banks, 1906.

Two species have been described in this genus, and these are known from eastern and central Asia.

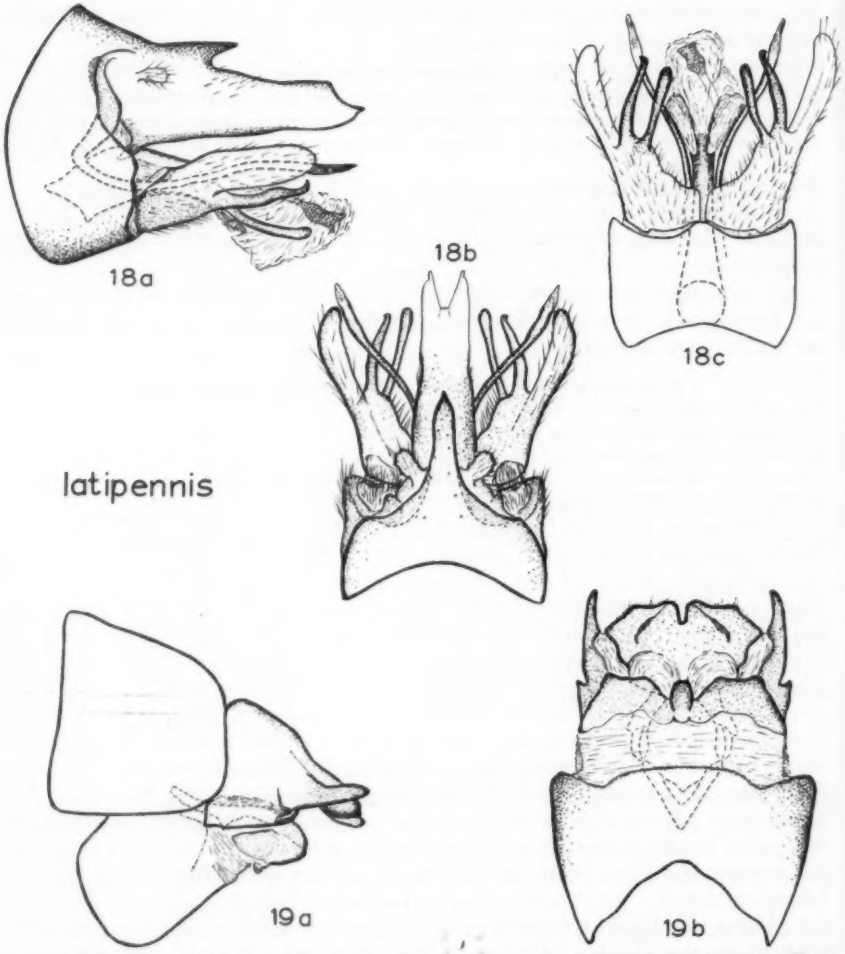
Phryganopsyche latipennis (Banks), new combination

Phryganea latipennis Banks, 1906, p. 107.
Phryganopsis latipennis Martynov, 1924, p. 211.
Phryganea (*Phryganopsis*) *latipennis* Tsuda, 1942, p. 309.
Phryganopsis latipennis subsp. Kimmins, 1950, pp. 698-705, Figs. 1-4.
Neuronia (*Phryganopsis*) *latipennis* Tsuda, 1951, p. 62, Fig. 59.

This species has been fully described by Kimmins (1950). Although it was known previously only from Honshu Island, Japan, Kimmins has recognized four subspecies, based on material from Assam, Sikkim and Burma, as well as Japan. The male genitalia of all of these forms are figured in his paper, but figures for the typical form *l. latipennis* from Japan are included here (Fig. 18) to provide a more complete account of the morphology of *Phryganopsyche*. The designation of these variants of the *latipennis* type as subspecies rather than species is entirely a matter of personal choice. No evidence of intergradation among these forms has been presented. The only data offered here on the resolution of this *latipennis* complex are derived from a single male specimen from Daibosatsu Pass, near Kofu, Japan, in which the genitalia (Fig. 20) are of the general *latipennis* type, although different from any of the four subspecies of *latipennis* recognized by Kimmins. In addition, the fore wings of this specimen are darker and more uniform golden brown than in the typical specimens of *latipennis* that I have seen from Japan. This indicates either that there is a good deal more variation in the Japanese population of *l. latipennis* than has been appreciated, or, what seems more likely, that there is more than one species of *Phryganopsyche* in Japan. This specimen is in the collection of Dr. Syoziro Asahina of Tokyo, Japan, who has very kindly made available much of the material used in this study.

Figures of the female genitalia are presented here, too (Fig. 19), because the only ones previously published (Ulmer, 1907) were based on a specimen that was not cleared and some of the significant details were, therefore, not shown. These include the membranous band across the subgenital plate, the short recessed median lobe at the apex of the subgenital plate, and the pointed lateral processes on the dorsum of the ninth segment which are joined to the median part by ventral membranous connections.

The larva of this species is figured in the first part of this paper and several of the external features have already been described. It can be added here that the gular sclerite (Fig. 7) is rather similar to the type occurring in some species of the Phryganeidae and Limnephilidae. The bristles shown on the humps of the first abdominal segment (Fig. 1) are seen, under magnification, to be stout, sharp spines, directed posteriorly (Fig. 6). In the specimens which I have seen



Figs. 18, 19. 18, Male genitalia of *Phryganopsyche latipennis*, 18a lateral view, 18b dorsal view (aedeagus omitted), 18c ventral view; 19, Female genitalia of *Phryganopsyche latipennis*, 19a lateral view, 19b ventral view.

the median, dorsal area of the first abdominal segment is not elevated to form a prominent dorsal hump as in most of the Phryganeidae and Limnephilidae. The abdominal gills are single (Fig. 1) and similar to those of the Phryganeidae in form, although in the absence of all but the ventral pair of gills on segments V, VI and VII, *P. latipennis* is different from any known phryganeid. The larvae I have seen are about 20 mm. long, but Tsuda (1951) gives the length of the mature larva as 28 mm. Presumably, then, the larva figured here is not a final instar. Tsuda (1951) has provided some interesting details concerning the habits of the larva. The larval case (Fig. 2) is constructed of a wide variety of plant materials, including mosses, leaves and stems of higher aquatic plants, pine needles, and occasionally with sand grains added. The larval case is two or three times as long as the larva itself, but is shortened prior to pupation. The larvae live in

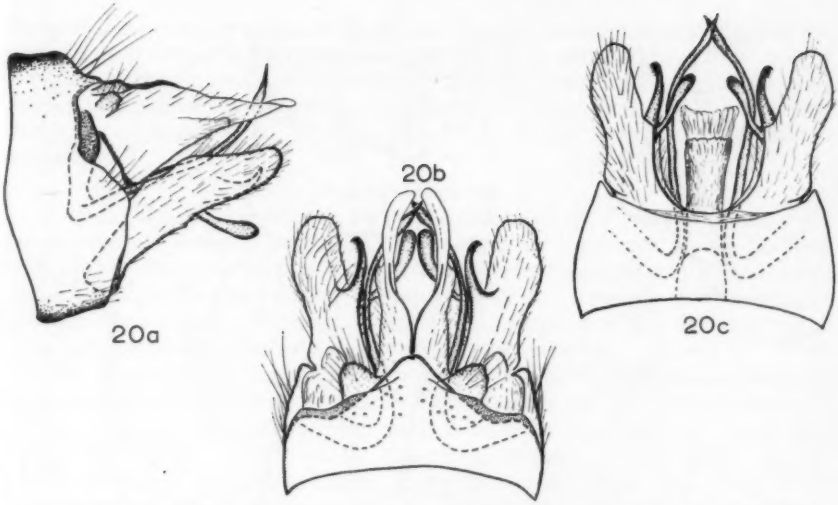


Fig. 20. Male genitalia of *Phryganopsyche* sp., 20a lateral view (aedeagus omitted), 20b dorsal view (aedeagus omitted), 20c ventral view.

quiet pools in the curves of streams where there are deposits of dead leaves on the bottom, and in springs, as well.

Figures of the whole adult insect of this species are available in at least two sources; a black and white drawing (Fig. 1154) in Iconographia Insectorum Japonicorum (ed. T. Esaki, 1950), and a colour photograph (Pl. 28, Fig. 428) in Takeuchi (1955).

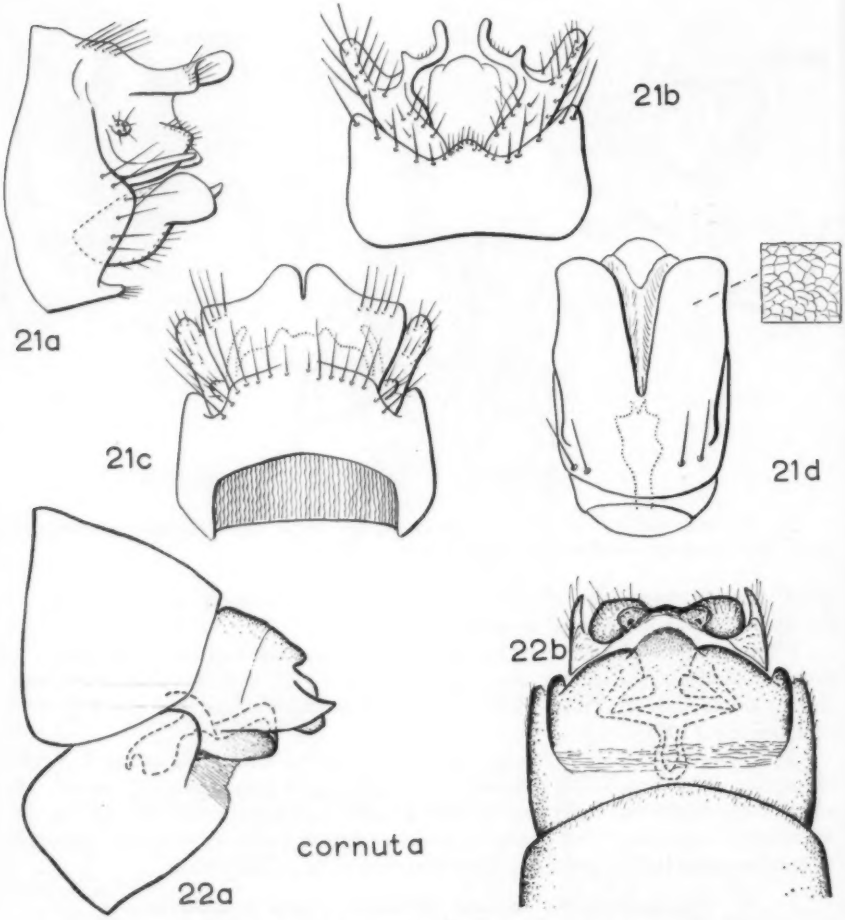
Martynov (1935) lists this species from the Amur River area of the U.S.S.R., basing the record on a single damaged specimen with only the wings intact. In view of the additional information, little as it is, that is now available on the distribution of species of this genus, it seems advisable to have complete specimens as confirmation before ascribing Martynov's record to *latipennis*.

***Phryganopsyche cornuta* (Kimmins), new combination**

Phryganopsis cornutus Kimmins, 1950, p. 704, Figs. 1-4.
Phryganopsis cornutus Kimmins, 1952, p. 174.

The colour and wing pattern of this species, known from Kambaiti, a mountainous locality in northeast Burma, are not greatly different from typical *latipennis*. The male genitalia have already been figured by Kimmins (1950), and Mr. Kimmins has kindly provided similar figures with additional details for inclusion in the present paper (Fig. 21). The male genitalia of the two species *cornuta* and *latipennis* are quite distinct, and the two can be readily separated by comparing Figs. 18 and 21.

Figures of the female genitalia were not given at the time of the original description, and these are presented here (Fig. 22), prepared from a paratype specimen kindly loaned to me by the Naturhistoriska Riksmuseum, Stockholm, Sweden. The female genitalia of *cornuta* show the same general features as those of *latipennis*. A similar membranous band extends across the subgenital plate and similar lobes occur on the posterolateral corners of the ninth tergum. Females of the two species can be readily distinguished, however, on the basis of the median lobe terminating the subgenital plate. In *latipennis* this lobe is narrow,



Figs. 21, 22. 21, Male genitalia of *Phryganopsyche cornuta* (figures by D. E. Kimmins), 21a lateral view, 21b ventral view, 21c dorsal view, 21d aedeagus enlarged; 22, Female genitalia of *Phryganopsyche cornuta*, 22a lateral view, 22b ventral view.

angulate and heavily sclerotized (Fig. 19b), while in *cornuta* the lobe is broad, evenly rounded and lightly sclerotized (Fig. 22b).

The immature stages of this species are unknown.

Summary

The generic name *Phryganopsis* Martynov, previously applied to a genus of Asian caddisflies, is shown to be preoccupied by a generic name in the Lepidoptera, and a new name *Phryganopsyche* is designated in its place. In the past this genus has always been considered a part of the family Phryganeidae because certain well-known characters occur in both groups. Although the pupal structures of *Phryganopsyche* are as yet unknown, analysis of a number of characters of larvae and adults indicates that this genus possesses at least sixteen characters which are unique and discordant among the known species of the Phryganeidae.

Many of these characters are, however, also found in such families as the Brachycentridae, Limnephilidae, and Lepidostomatidae, while others appear to be unique in the Trichoptera. Since no single family now recognized encompasses the set of characters possessed by this genus, a new family of Trichoptera, the Phryganopsychidae, is created for it. Present knowledge of the species now known is summarized.

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Spruce Budworm Parasite Studies in Northwestern Ontario[1]

By B. M. McGugan[2] and J. R. Blais[2]

Introduction

The extensive coniferous stands in northwestern Ontario have been subjected to repeated widespread outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.) (5). About 1939 two such outbreaks originated almost simultaneously, one on the west shores of Lake Nipigon and the other south of Lac Seul approximately 180 miles farther west. Each outbreak eventually covered thousands of square miles and was responsible for the destruction of hundreds of square miles of balsam fir forest. Studies of the parasite complex attacking the spruce budworm in northwestern Ontario and the assessment of its general influence on budworm population trends were initiated in the Lake Nipigon outbreak in 1946 by Professor N. R. Brown, now of the University of New Brunswick, and were further developed by the senior author from 1947 to 1950. Similar investigations were initiated by the junior author in the Lac Seul outbreak in 1950 and continued until 1954. Studies in both areas were continued on a limited basis until 1956 through the co-operation of several research officers.

The Lake Nipigon studies covered the peak of the outbreak from 1946-48, the period of rapid decline in 1949-50, and the gradual and erratic return to near endemic conditions by 1956. In contrast, the Lac Seul outbreak has continued on an ever-increasing scale until the present time (30); in the study areas, observations coincided with the period of high population levels that caused near complete host tree mortality by 1956 (6). Tree mortality resulting from repeated severe defoliation was in evidence near the epicentres of the two outbreaks when the studies were initiated and was very widespread when they were terminated.

Relatively little of the extensive literature on the spruce budworm deals with insect parasites as natural control agents. Seven papers include attempts to appraise the incidence of parasites in field populations. Tothill (32) compared quantitatively and qualitatively the parasite complex in New Brunswick and British Columbia and recommended the importation of *Phytodietus fumiferanae* Rohw. as a possible remedy for the serious outbreaks in eastern Canada. Wilkes and Anderson (37) and Wilkes *et al.* (38) analysed data derived from collections made in British Columbia to obtain parasites for release in eastern Canada and from collections made at liberation points. Their method of analysis was simply to express the relative occurrence of all parasites in terms of the total number of hosts collected during the season. The derivation of the total expressions of parasitism given by Daviault (13) for two points in Quebec between 1945 and 1947 cannot be appreciated from his presentation but the increased abundance of *Meteorus trachynotus* Vier. during 1947 is particularly noteworthy. Dowden *et al.* (15) and Dowden and Carolin (16), dealing with spruce budworm outbreaks in the Adirondack region of New York State, studied the incidence of parasites at a number of points. Aggregate percentages of mortality based on methods adapted from Thompson (31) were remarkably high and considered indicative of the major role of parasites in the rapid decline of the outbreak in 1947 and 1948. Jaynes and Drooz (19) using a similar ap-

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proach studied the incidence of parasites in a spruce budworm outbreak in Maine between 1948 and 1951 and concluded from the increasingly higher aggregate percentages of parasitization that parasites were a major factor in the rapid decline of the outbreak.

In the present paper the parasite complex in northwestern Ontario is discussed and compared with that reported for other outbreak regions. Data on the occurrence of parasites in the two outbreak areas are presented separately and in relation to the known history of the outbreaks and to the available information on spruce budworm population levels. Some conclusions are drawn on the impact of the parasite complex as a whole and of certain of its elements.

Methods

The experimental plan employed was to collect and rear periodic samples of budworms taken at predetermined periods of development from areas chosen to represent two basic stand types and various locations with respect to the origin and limits of the outbreaks. The type of plots, collection schedules, rearing procedures, determination of parasites, and the analytical treatment of the data are outlined briefly below.

Plots, Collections, and Rearing Procedures

The same general principles were followed in both study areas but a number of variations were imposed by local conditions and the availability of spruce budworm material. Only the significant variations are mentioned.

Ten different plots were used, six in the Nipigon area and four in the Lac Seul area, but not all were used in any one year. The majority of the plots were in mature to overmature stands with a predominance of balsam fir, but which included various amounts of white spruce and black spruce. Decadent white birch and trembling aspen were also minor components. A few plots were in young coniferous reproduction stands in which open-grown balsam fir trees less than 30 feet in height predominated. The plots were not delimited as to area but rather consisted of marked balsam fir trees that were considered typical of the general stand. In one of the Lac Seul plots foliage was collected from mature white spruce trees to compare the parasite complex with that found on balsam fir.

Budworm material was collected from 18-inch branch tips removed from the mid-crowns of the trees. The number of branch tips taken during any collection depended on the number of insects present and was designed to yield from 200 to 400 insects. All insects found on the foliage collected were placed in rearing to avoid any bias. The homogeneity of the Nipigon plots with respect to the incidence of parasites was checked by dividing the series of marked trees in each plot into sub-groups and by maintaining all subsequent records on this basis. Spruce budworm population data in the form of egg counts and defoliation estimates were available for areas immediately adjacent to the Nipigon plots from the unpublished records of Fettes (17) and others; similar records were maintained for the Lac Seul plots.

The principle of making collections at predetermined periods of host development is considered one of the important aspects of this study, and has since been discussed by Miller (23). There is an optimum time to assess the incidence of each species of parasite but it is hardly practical to attain this for even the more important species under field conditions and some compromise collection schedule must be adopted. The somewhat empirical system of four collections developed in the early years of the Nipigon studies proved adequate for

all parasites except the egg parasite, *Trichogramma minutum* Rly. The four collections were made as follows:

1. When the bulk of the population was in the fourth instar. This collection assessed the occurrence of parasites which attack the host during the late summer and overwinter therein (primarily *Apanteles* and *Glypta*).
2. When the bulk of the population was in the fifth instar. This collection confirmed the abundance of the early larval parasites mentioned above and indicated the sequence of attack of the late larval parasites.
3. Late in the sixth instar when the first pupae appeared. This timing coincided with the maximum abundance of the late larval parasites.
4. Late in the pupal period shortly after adult emergence began. This collection measured the incidence of pupal parasites.

The second collection as defined above was found to be non-essential and was discontinued in both study areas after 1950. Although the egg parasite, *Trichogramma minutum* Rly., was present in both study areas no special efforts were made to measure its incidence. The examination of large numbers of egg masses each year during the course of population counts and other biological studies indicated that this parasite was rare.

Insects were reared in 8-ounce screw-top jars using balsam fir shoots as food. In the Nipigon studies larvae were classified as to instar and sex at the time of collection and each category was reared as a group keeping all subsequent stages separate. In all cases laboratory-reared and field-collected pupae were kept separate. These methods allowed parasite incidence to be associated with the stage of the host both at the time of collection and at the time of parasite emergence. This information helped confirm the validity of the collection schedule and provided other interesting data on the influence of parasites on host development (22).

Determination of Parasites

Parasites were tentatively identified as recovered from cocoon or puparial characteristics. The preliminary identifications of hymenopterous parasites were in excellent agreement with adult determination supplied later by officers of the Entomology Research Institute and made it reasonable to assume that the preliminary identifications of the few specimens which did not emerge as adults were valid. Considerable difficulty was experienced in obtaining satisfactory adult emergence of dipterous parasites. Puparia were identified from a key prepared by Ross (29) and by comparison with material in the reference collection at the Forest Insect Laboratory, Sault Ste. Marie, Ontario. The few adults obtained were examined by officers of the Entomology Research Institute.

Analytical Methods

The expression and appraisal of mortality caused by parasites and other control factors in field populations is an exceedingly complex subject. Great strides have been made in recent years with particular reference to forest insects by Morris and others (24, 25, 26, 27). The conclusions Morris has drawn are based on sampling methods and concepts that were largely conceived and evolved after the present studies were undertaken. During the early years of the present studies the extreme importance of frequent population measures was not fully appreciated and the appraisal of all mortality factors was not considered feasible under field conditions. However, there was a real need for a general appreciation of the incidence of parasites through the peak and terminal

years of a large-scale outbreak in a major pulp producing area. The highly organized collection and rearing schedules described above gave reliable estimates of the apparent mortalities caused by the important elements of the resident parasite complex during the years of study. Unfortunately, only limited information of a relative character is available for the population levels of the spruce budworm over the same period and no specific attempts were made to measure other sources of mortality. The most suitable analytical technique for this type of data was the Mortality/Survival ratio approach of Bess (4). Morris (25) has recently shown that some of the assumptions inherent in this approach are subject to severe doubt at least for spruce budworm studies and that the combination of individual ratios for different parasites does not necessarily express the relative effectiveness of parasites from generation to generation. The nature of the data available from the present studies precludes the possibility of a more comprehensive analysis. However, the data do contain considerable information on parasitism during a major outbreak and the general trends as expressed by M/S ratios have a gross similarity to results from other outbreaks. Only generalized observations will be drawn from M/S ratios and attention will be focused primarily on variation rather than on magnitude.

M/S ratios are obtained by dividing the number of individuals destroyed during any stage or at any time by the number that escaped death. Consequently, they express the reduction in host population in terms of an individual survivor. Methods following certain broad assumptions are available for combining M/S ratios and for converting them to mortality percentages. The results obtained can only be considered broadly indicative of the role of parasites in the population dynamics of the host insect. Further precision can only be obtained by the more onerous life table approach that has come into vogue in recent years.

The application of the M/S ratio technique to the present data requires some elaboration. The initial step was to convert parasite incidence to more readily appreciated percentages. Generally, these were calculated for each species in each collection although certain dipterous species were grouped because of their sporadic occurrence. The assumptions underlying these calculations were as follows:

1. Larvae accidentally killed, lost, or dead of unknown causes were assumed to have contained an equal proportion of parasites as those surviving these hazards. Accordingly, the numbers in the original sample were decreased by the number of such insects.
2. Larvae parasitized by *Apanteles* and *Glypta*, which attack very early larval stages (9, 10), have been shown to be materially retarded in size and rate of development (22) and were not considered available hosts for parasites attacking ultimate and penultimate instars. The occurrence of these later parasites was calculated by not only reducing the original sample by those that died of unknown causes but also by the number that gave rise to *Apanteles* and *Glypta*.
3. The samples of field collected pupae were assumed to be the best basis for calculating the incidence of parasites which attack pupal or prepupal stages. Pupae that died were dissected to establish the presence or absence of parasites.

The mortality percentages for each species were examined in the light of the time of the collection and the biology of the parasite. The percentage most representative of the occurrence of the species during that particular season was

TABLE I
Mortality/Survival Ratios as Calculated from Typical Rearing Data

Parasite	Percentage parasitism in collection:[1]				Mortality/survival ratios for life history periods:[2]		
	1	2	3	4	EL	LL	P
Apanteles	**6.3**	2.3	–	–	0.070	–	–
Glypta	**3.9**	4.9	4.7	0.3	0.043	–	–
Meteorus	–	1.0	**28.0**	31.4	–	0.52	–
Lypha	–	5.6	**7.7**	0.9	–	0.14	–
Omotoma	–	–	**1.8**	0.6	–	0.033	–
Diptera (misc.)	–	1.7	**8.1**	0.9	–	0.15	–
Apechthis	–	–	–	**8.7**	–	–	0.10
Itoplectis	–	–	–	**1.1**	–	–	0.013
Phaeogenes	–	–	–	**5.4**	–	–	0.064
Unknown	–	–	–	**0.5**	–	–	0.006
					0..11	0..84	0..19

Total M/S ratio = EL + LL + (EL) (LL) + P + P [EL + LL + (EL) (LL)] = 1.43.

$$\text{Total Mortality} = \frac{1.43}{1.43 + 1} = 59 \text{ per cent.}$$

[1]Percentages in bold face are those chosen as most representative.
[2]EL = early larval; LL = late larval; P = pupal period.

chosen. Earlier samples were considered as taken before the completion of attack by the parasite and later samples as taken after the parasite began to emerge. The full series of four collections gave more latitude in this regard.

The methods used in calculating M/S ratios and total mortality are shown in Table I. The percentages for all species in all collections are shown and those chosen as representative are in bold face type. The selected percentages are converted to M/S ratios within three broad groupings wherein the different parasite species are considered to have acted on the host population concurrently. The groupings are referred to as early larval (EL), late larval (LL), and pupal (P). The M/S ratios for these three groups are obtained by direct addition which implies that contemporaneous parasites act completely independently which may or may not be the case. The final step is to combine these group ratios to yield a total ratio using a procedure which assumes that those parasites comprising a group react on the residual population left by the previous group. This is obviously a broad assumption but in the absence of measures of other mortality factors it is the only recourse possible. In the example given in Table I the total M/S ratio is 1.43 which means that during the interval under study (late fourth instar to adult emergence) 1.43 individuals died as a result of parasitism for every individual that reached the adult stage. This is equivalent to stating that 59 per cent of the population at the fourth instar failed to reach the adult stage because of parasitism.

The above analytical technique has been applied to data from all plots and the results form the basis of the observations and trends discussed in the remaining sections of this paper.

Results

Parasite Complex

A great number of parasites have been reported as reared from the spruce budworm but many species are of questionable importance and doubtful status.

In 1948 Dowden *et al.* (15) and Wilkes *et al.* (38) published listings of their own and published records of spruce budworm parasites. In 1950, Dowden and Carolin (16) consolidated these lists and added eight new records to bring the recorded total to 78 species. Several additional records have since been published: Daviault (13) added *Clinocentrus* sp. and *Sarcophaga tetra* Ald.; Burks (11), *Syntomosphyrum esurus* (Ril.); Arthur & Coppel (1), *Sarcophaga aldrichi* Park.; Krombein *et al.* (20), *Apanteles petrovae* Wly. and *A. polychrosidis* Vier.; and Townes & Townes (33) *Chorinaeus longicalcar pleturus* Davis, *C. l. talaris* Townes, *C. excessorius* Davis, and *Exochus nigripalpis tectulum* Townes. The published records known to the present authors therefore total 88 species and include 36 ichneumonids, 16 braconids, 17 chalcidoids, 13 tachinids, 4 sarcophagids, 1 cecidomyid, and 1 muscid. Of these, specific determinations of 9 ichneumonids, 7 braconids, 11 chalcidoids, 2 tachinids, 1 sarcophagid and the cecidomyid were not available at the time of listing and may include either duplicate results or species subsequently described by such authors as Townes & Townes.

When all known or suspected hyperparasites are excluded from the parasite species reared from the spruce budworm in the present studies, the complex was composed of 30 species that included 10 ichneumonids, 7 braconids, 3 chalcidoids, 7 tachinids, and 3 sarcophagids (Table II). Four of the species listed in Table II have not previously been reported as parasites of the spruce budworm: *Horogenes conodor* Vier.; two undesignated *Apanteles;* and a new species of *Synetaeris* to be described by G. S. Walley. Walley (personal communication) states that some of the *Horogenes* specimens collected by Coppel (12) in British Columbia are the same as the *Synetaeris* n. sp. material obtained from the Nipigon plots. Wilkes *et al.* (38) were therefore incorrect when they assumed that Coppel's material was equivalent to *H. cacoeciae* as listed previously by Dowden *et al.* (15). The undesignated species of *Apanteles* were determined by W. R. M. Mason as "*polychrosidis* group" and "*cacoeciae* group"; the former could be equivalent to *A. polychrosidis* as recorded by Krombein (20). These new records bring the reported total of possible parasites of the spruce budworm to 92. It is quite possible that the numerous non-specific determinations given in the literature contain many duplicate records that would affect this total.

A number of species considered to be hyperparasites occurred in small numbers. *Gelis tenellus* (Say), *Mesochorus* sp., and *Tetrastichus* sp. were the most common and have all been recorded previously. A few specimens of *Tetrastichus coerulescens* Ashm., *Elasmus atratus* How., and *Pediobius tarsalis* (Ashm.) were also reared and considered to be hyperparasites. The primary parasites affected were mainly *Meteorus, Apanteles,* and *Glypta.*

The great differences in the constancy with which species were recorded as parasites of the spruce budworm in northwestern Ontario are shown in Table II. The occurrence ratings allow division of the complex into three groups termed characteristic, common, and occasional parasites of the spruce budworm. When these ratings are compared with those of authors working in other regions, considerable uniformity is evident. Dowden *et al.* (15) drew attention to the similarities in the parasite complex between New England and Colorado and rated the 36 species obtained in New England as abundant – 10, common – 3, present – 4, and rare – 19. Of the 13 species listed as characteristic or common in the present study, 11 were the same as those rated as abundant or common by Dowden. In the present study *Lypha* and *Agria* are rated as characteristic and common while Dowden listed them as rare. In contrast, *Horogenes cacoeciae* and *Dicladocerus* classed as common and abundant by Dowden were an occasional

TABLE II
Primary Parasites Reared from the Spruce Budworm during studies at Lake Nipigon, 1947-54 and at Lac Seul, 1950-54

	Nipigon Plots (6)										Lac Seul Plots (4)							Occurrence Rating*	Group No.**
	1947	1948	1949	1950	1951	1952	1953	1954	1955	1950	1950	1951	1952	1953	1954	1955	1956		
No. of Plots in Use	3	2	3	3	1	2	2	3	1	1	2	2	4	4	4	2	1		
Parasite Species																			
HYMENOPTERA																			
Ichneumonidae																			
Apechthis ontario (Cress.)	x	x	x	x	–	x	x	x	x	–	x	x	x	x	x	x	–	0.80	I
Campoplex sp.	–	–	–	–	x	–	–	–	–	x	–	–	–	–	–	–	–	0.05	III
Exochus sp.	–	–	–	x	x	x	–	x	–	–	x	–	–	–	–	–	–	0.12	III
Glypta fumiferanae (Vier.)	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	0.95	I
Horogenes cacoeciae (Vier.)	–	–	x	–	–	–	–	x	–	–	–	–	–	–	–	–	–	0.05	III
Horogenes conodor (Vier.)	–	–	–	–	–	–	–	–	–	–	–	–	x	x	x	–	–	0.12	III
Itoplectis conquisitor (Say)	x	x	x	x	–	x	x	x	–	–	x	x	x	x	x	x	–	0.75	I
Itoplectis quadricingulatus (Prov.)	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	x	–	0.05	III
Phaeogenes hariolus (Cress.)	x	x	x	x	–	x	x	x	x	–	x	x	x	x	x	x	–	0.73	I
Synetaeris sp.	–	–	–	x	x	x	–	–	x	x	–	–	–	–	–	–	–	0.20	III
Braconidae																			
Apanteles fumiferanae Vier.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	0.98	I
Apanteles petrovae Wly.	–	–	–	x	x	–	–	–	–	x	–	–	–	–	–	–	–	0.10	III
Apanteles spp.	–	–	–	x	–	–	–	–	–	x	–	–	x	x	–	–	–	0.15	III
Eubadizon sp.	–	–	–	x	x	x	–	–	–	–	x	x	x	–	–	–	–	0.22	III
Macrocentrus iridescens French	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	0.02	III
Meteorus trachynotus Vier.	x	x	x	x	–	x	x	x	x	x	x	x	x	x	x	x	x	0.95	I
Chalcidoidea																			
Amblymerus verditer (Nort.)	x	x	x	–	–	x	x	x	x	–	–	x	x	–	x	x	–	0.42	II
Psychophagus tortricis (Brues)	x	x	x	–	–	–	x	x	x	–	x	–	–	–	–	–	–	0.30	II
Syntomosphyrum esurus (Ril.)	–	–	–	–	–	–	–	–	–	–	–	–	–	x	x	–	–	0.05	III

TABLE II—Continued

	Nipigon Plots (6)										Lac Seul Plots (4)							Occurrence Rating*	Group No.**
	1947	1948	1949	1950	1951	1952	1953	1954	1955	1956	1950	1951	1952	1953	1954	1955	1956		
No. of Plots in Use	3	2	3	3	1	2	2	3	1	1	2	2	4	4	4	2	1		
DIPTERA																			
Tachinidae																			
Actia interrupta (Curr.)	–	–	x	x	x	x	–	x	x	–	–	–	x	x	–	–	–	0.25	III
Eumea caesar (Ald.)	x	x	x	x	–	x	x	x	x	x	–	–	–	–	–	x	x	0.52	II
Lypha setifacies (West.)	x	x	x	x	x	x	–	–	–	–	x	x	x	x	x	x	–	0.75	I
Nemorilla pyste (Wlk.)	x	x	x	–	–	–	–	–	–	–	x	–	–	–	–	x	–	0.17	III
Omotoma fumiferanae (Tot.)	x	x	x	x	–	x	–	–	x	–	x	x	x	x	x	x	x	0.77	I
Pseudoperichaeta erecta (Coq.)	–	x	x	x	–	–	–	–	x	–	–	–	–	–	–	x	–	0.15	III
Phryxe pecosensis Tns.	x	x	x	x	–	x	x	x	x	–	–	–	x	–	–	x	–	0.50	II
Sarcophagidae																			
Agria affinis (Fall.)	x	x	–	–	–	x	–	x	–	–	x	x	x	–	–	x	–	0.30	II
Sarcophaga aldrichi Park.	–	–	–	–	–	–	–	x	–	–	–	–	–	–	x	–	–	0.07	III
Sarcophaga sp.	–	x	–	–	–	–	–	x	x	–	–	–	–	–	–	–	–	0.12	III

*Ratings are based on the number of plot-year occurrences divided by the total number of possible plot-year occurrences.

**Group I. Occurrence rating 0.70 and under
Group II. Occurrence rating 0.30-0.69
Group III. Occurrence rating less than 0.30

parasite and absent respectively in northwestern Ontario. Only five of the less common species reported for each area were the same. Wilkes *et al.* (38) dealing with the spruce budworm in British Columbia where the parasite complex might be expected to be markedly different from the east, rated 15 species as the important elements of the complex. Six of these, *Apechthis, Glypta, Apanteles, Lypha, Omotoma,* and *Phaeogenes* were characteristic parasites in northwestern Ontario and two, *Phryxe* and *Agria* were common. Of the remaining seven species, *Phytodietus fumiferanae* Rohw. and *Ceromasia auricaudata* Tns. are restricted to western North America and three species occur only rarely in eastern Canada.

The important elements of the spruce budworm parasite complex are obviously quite uniform regardless of the location in North America. However, each area where intensive studies have been made has produced a somewhat different list of parasites that attack the spruce budworm occasionally. This is well illustrated in the comparisons between northeastern United States and northwestern Ontario. Intensive rearings in other localities will undoubtedly produce somewhat different lists including a few new records. However, the characteristic parasites in any outbreak will be drawn from the 12 to 15 species noted above.

Although the important elements of the parasite complex are superficially quite similar throughout the range of the spruce budworm in North America, Table II shows that noteworthy differences existed between the study areas in northwestern Ontario. The most striking difference concerns the relative paucity of the Diptera complex in the Lac Seul outbreak. *Actia, Eumea, Pseudoperichaeta* and *Phryxe,* were common parasites in the Nipigon plots but were comparatively rare in the Lac Seul area. Similarily, the primary polyembryonic chalcids, *Psychophagus tortricis* (Brues) and *Amblymerus verditer* (Nort.), were regularly found in the Nipigon study areas and occasionally in extreme abundance while they were only rarely recorded from Lac Seul rearings.

Several of the rare elements of the parasite complex listed in Table II were only recorded from one of the outbreak areas. An interesting example concerns the species of *Horogenes. H. conodor* was obtained only in the Lac Seul rearings while *H. cacoeciae* and an undescribed species of the closely related genus *Synetaeris* were found only in the Nipigon plots. These latter two species, as well as such other rare components of the Nipigon complex as *Eubadizon* and *Exochus,* were not observed until 1950 when spruce budworm numbers reached a low level following a period of high abundance. Apparently such species are characteristic of endemic populations or they attack the budworm only incidentally and therefore have a better chance of appearing in rearings when budworms are collected with difficulty.

The absence of Nipigon records for the common pupal parasites in 1951 reflects the fact that only one plot was studied and only a small number of pupae could be obtained for rearing. The appearance of *Sarcophaga aldrichi* in both study areas in 1954 is of some interest. This is the dominant parasite in Ontario of the forest tent caterpillar, *Malacosoma disstria* Hbn., which was in outbreak proportions in both study areas for several years preceding 1954. These tent caterpillar outbreaks declined markedly in 1953 and had disappeared by 1954 leaving an abundance of *S. aldrichi.* Apparently some of the parasites were able to maintain themselves by attacking the spruce budworm despite its appearance several weeks later in the season than the tent caterpillar.

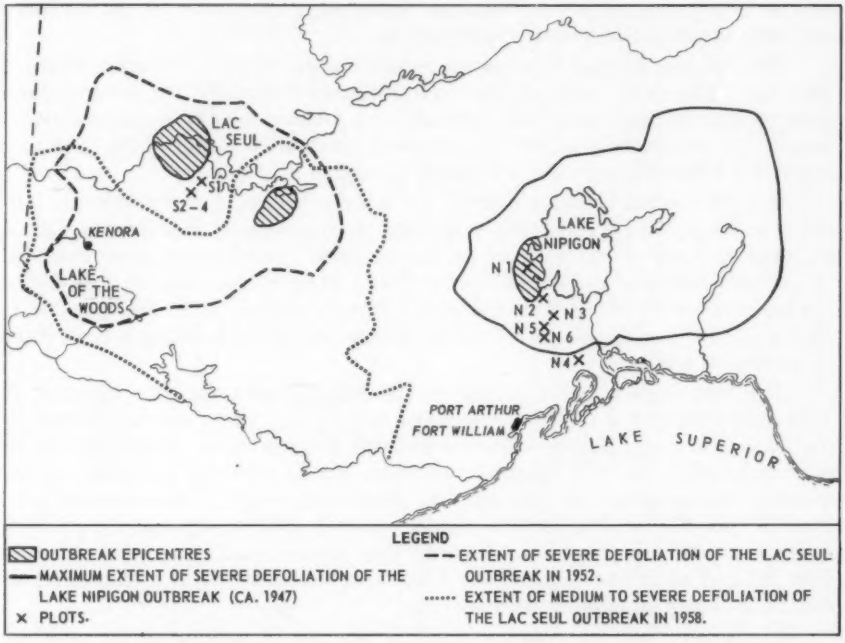

Fig. 1. Map of northwestern Ontario showing the Lake Nipigon and Lac Seul spruce budworm outbreak areas.

The Lake Nipigon Outbreak

The parasite study plots in the Nipigon area were chosen to represent different infestation histories as reflected by their location in reference to the focal point of the outbreak and two different forest types. Balsam fir was the predominant tree species in all plots. Some plots were located in mature stands recognized to be highly susceptible to budworm attack while others were in young vigorous reproduction stands. Plot locations in relation to both geographic features and the ultimate limits of the outbreak are indicated in Fig. 1 while further details as to their composition, infestation history, period of study, and the eventual impact of the outbreak are outlined briefly in the following paragraphs.

Plot N1 was located in a stand of fir reproduction near the centre of the Nipigon outbreak where severe defoliation began at least as early as 1939 and the first mortality of mature trees was recorded in 1944. When the plot was established in 1946 the surrounding mature stands were already dead or dying. Observations were maintained for two years and then the plot was abandoned because of the condition of the trees.

Plot N2 was also in a reproduction stand but was located some 50 miles from the centre of the outbreak. When established in 1946, the boundary of severe infestation was just south of the plot. The trees were first severely defoliated in 1944 and near complete defoliation of the current year's growth followed in 1945 and 1946. Subsequently, defoliation declined rapidly until by 1949 it was of little consequence. With some effort it was possible to maintain observations on the parasites present until 1951. The stand has recovered remarkably well

and in 1958 presented a very vigorous appearance. Evidence of the outbreak was only apparent upon careful examination.

Plot N3 was located in a mature spruce balsam stand a few miles south of Plot N2. The early stages of the outbreak were essentially the same in both plots except that near complete defoliation of current growth began somewhat earlier and continued into 1947 in this more susceptible stand. Tree mortality began the following year and was nearly complete by 1951.

Plot N4 was not established until 1949 when it became apparent that the outbreak had reached its maximum extension. It was located in a mature balsam fir stand near the southern limits of the outbreak. Defoliation never exceeded 80 per cent and only approached this in 1947. No tree mortality attributable to the budworm was recorded in this plot. Parasite studies were only possible in 1949 and 1950 during the main outbreak period and in 1954 during a resurgence in budworm numbers.

The first evidence of a decline in the Nipigon outbreak was apparent in 1948 and by the end of 1949 insect numbers had reached a very low level throughout the entire area. This condition continued through 1950. Population levels increased slightly in 1951, primarily on white spruce trees and in a few residual stands of living balsam fir trees near the southwest corner of the outbreak area. Plots N5 and N6 were selected in mature stands in 1952 to appraise the parasites in these localized populations. Records were discontinued after three years in Plot N5 and after five years in N6 when tree mortality made it impossible to collect an adequate number of budworms.

In summary, one reproduction plot was near the focal point of the outbreak where all balsam fir trees were killed; a reproduction and a mature plot were some distance from the epicentre but within the area where tree mortality in susceptible stands was virtually complete; one mature plot was on the periphery of the outbreak where high population levels were present for an insufficient time to cause tree mortality; and two mature plots were in areas of resurgence that followed the collapse of the outbreak. Parasite data were not obtained from all plots in all years. Plot selection and the number used at any time depended on the course of the infestation, tree mortality, and the amount of field assistance. The number of budworms collected and reared each year by plot are indicated in Table III.

During the early years of the Nipigon studies considerable attention was paid to intra-plot variability in parasite occurrence. Intra-plot tests of homogeneity using the Chi-square test were made on the sub-plot data with as many as nine different parasite species from a plot and including examples of early larval, late larval, and pupal parasites. Nearly 80 tests were performed and five yielded significant values of Chi-square; one more than would be expected by chance alone. The five cases were distributed among the various plots and in no case was there a consistent difference in the occurrence of any parasite over a period of years or in any plot. With the collecting methods employed, each plot was apparently a homogeneous universe for sampling the occurrence of spruce budworm parasites.

Individual and total M/S ratios were calculated for each plot for each year according to the analytical methods described earlier. In these analyses only the more abundant dipterous parasites, *Lypha* and *Omotoma*, were treated individually; the remainder were treated as a group. A small number of unemerged hymenopterous specimens were classified as unknown. The resultant ratios for

TABLE III

A summary of spruce budworm larvae and pupae collected and reared from collection plots in northwestern Ontario, 1946-56.

Nipigon Outbreak:

Coll'n No.	Plot N1		Plot N2						Plot N3					Plot N4			Plot N5			Plot N6				
	1946	1947	1946	1947	1948	1949	1950	1951	1946	1947	1948	1949	1950	1949	1950	1954	1952	1953	1954	1952	1953	1954	1955	1956
1	332	380	205	400	–	148	273	53	201	390	–	122	255	155	145	143	260	163	300	86	300	305	251	150
2	–	400	200	400	294	369	294	–	204	400	355	388	206	335	216	–	–	202	–	–	–	–	–	–
3	164	408	195	415	281	375	352	101	121	475	317	350	158	315	205	150	279	178	230	137	211	335	265	100
4	1276	560	285	512	316	359	74	29	91	500	415	338	13	187	84	295	209	62	254	196	30	351	138	6
	1772	1748	885	1727	891	1251	993	183	624	1765	1087	1198	632	992	650	588	748	605	884	419	541	991	654	256
	3520		5747						5306					2230			2137			2861				

Grand Total — 21,801

Lac Seul Outbreak:

Coll'n No.	Plot S1							Plot S2						Plot S3			Plot S4		
	1950	1951	1952	1953	1954	1955	1956	1950	1951	1952	1953	1954	1955	1952	1953	1954	1952	1953	1954
1	400	501	504	405	400	292	210	400	1002	595	400	600	279	309	300	557	251	240	400
2	400	–	–	–	–	–	–	400	–	–	–	–	–	–	–	–	–	–	–
3	417	501	275	317	375	251	267	405	1070	310	349	360	251	307	263	375	170	355	375
4	812	870	296	299	229	248	63	626	1140	440	267	378	286	283	314	410	366	365	390
	2029	1872	1075	1021	1004	791	540	1831	3212	1345	1016	1338	816	899	877	1342	787	960	1165
	8332							9558						3118			2912		

Grand Total — 23,920

the more common parasites and the total ratios are presented in Table IV. The various columns are not additive because of the analytical procedure and the omission of certain minor species and miscellaneous groups. The results for 1946 were derived from records compiled by N. R. Brown; the present analytical procedure was not considered in the collection of these earlier data and a liberal translation was necessary for present purposes.

Correlations between M/S ratios and the course of the budworm outbreak are difficult to assess without reference to some quantitative index of host population level. Annual defoliation estimates and egg mass densities have been compiled by Fettes (17) and others for the same plots or areas immediately adjacent to them. Egg densities represent the better criterion for comparison with M/S ratios but unfortunately these records are not as complete as the defoliation records. The defoliation history is therefore the best source of comparison available and is shown with the M/S ratios for each plot in Fig. 2. A discussion of the sequence of events in each plot follows.

Although parasite observations at Plot N1 were restricted to 1946 and 1947, two points are worthy of note. The lowest total M/S ratios obtained before the general collapse of the outbreak were from this plot and are indicative of the minor influence of parasites near the centre of the outbreak. Interestingly, *Meteorus* was the most prevalent parasite at Plot N1 in 1947 and was more common there than at any other plot sampled that year. This is perhaps the earliest indication of the striking build-up of this parasite in 1949 and 1950.

At Plot N2, another reproduction area, the first indication of a general decline was evident in the reduced defoliation of 1947, a year earlier than in other plots in the same intermediate area of the outbreak. This downward trend in defoliation continued through 1948 and 1949 and was accompanied by striking changes in parasitism. In 1948, large numbers of a chalcid, *P. tortricis* Brues, combined with less spectacular increases by other species greatly increased the total effectiveness of parasites. The near absence of the chalcid in 1949 reduced the M/S ratio to a value only appreciably higher than in 1947. In 1950, further increases in parasitism, particularly by *Meteorus* raised the M/S ratio to the highest value obtained during these studies. The M/S ratio was appreciably lower in 1951 but still at a high level while the host density reached a very low level. It became unpractical to collect budworms in subsequent years and the young vigorous balsam fir trees quickly recovered showing little effect of the outbreak.

At Plot N3 the 1947 egg density was sufficient to produce a high population level in 1948. However, this did not materialize and defoliation dropped from near 100 per cent to somewhat less than 60 per cent in 1948. The M/S ratio was more than double that for 1947 and somewhat higher than the value derived for 1946. This increase probably indicates that parasites contributed to the lessened defoliation and to the much reduced egg density recorded in the fall of 1948. In 1949, the budworm population level continued to fall while the M/S ratio remained essentially the same despite a marked increase by *Meteorus*. In 1950, the budworm population level was very low and the M/S ratio reached a high level due to the rather spectacular numbers of *Meteorus*, as already mentioned for Plot N2. Despite the reduced numbers of budworms tree mortality continued until essentially complete by the end of 1951.

Fig. 2 indicates that the course of the infestation at Plot N4 was markedly different from the plots discussed above. Defoliation was never complete and was most severe in 1947 when it reached 80 per cent. In the years that followed,

TABLE IV

Mortality/Survival Ratios for the more common parasites obtained from spruce budworm collection plots in northwestern Ontario, 1946-56.

Nipigon Outbreak:

Parasite	Mortality/Survival Ratios: Plot N1		Plot N2						Plot N3					Plot N4			Plot N5			Plot N6				
	1946	1947	1946	1947	1948	1949	1950	1951	1946	1947	1948	1949	1950	1949	1950	1954	1952	1953	1954	1952	1953	1954	1955	1956
Apanteles	0.18	0.030	0.36	0.23	0.32	0.18	0.32	2.0	0.18	0.086	0.072	0.054	0.065	0.14	0.023	0.048	0.080	–	0.044	0.080	0.017	0.10	0.006	0.093
Glypta	0.061	0.2	0.039	0.25	0.19	0.10	0.009	0.20	0.183	0.12	0.089	0.054	0.036	0.091	0.011	–	0.053	0.006	0.030	0.020	–	0.041	0.089	0.029
Synetaeris sp.	–	–	–	–	–	–	0.042	–	–	–	–	–	0.18	–	0.17	0.042	–	–	–	–	–	–	0.006	–
Meteorus	0.018	0.15	0.023	0.10	0.51	0.23	3.8	0.021	0.13	0.10	0.35	0.68	2.1	0.59	0.53	0.018	0.075	0.006	0.099	0.018	–	0.064	1.5	0.23
Lypha	0.048	0.004	0.009	0.012	0.027	0.052	0.042	0.021	0.023	0.17	0.12	0.16	0.18	0.059	0.088	0.003	0.010	–	–	0.005	–	–	–	–
Omotoma	0.048	0.099	0.040	0.040	0.048	0.080	0.28	–	0.031	0.039	0.035	0.036	0.058	0.044	0.022	–	–	–	–	–	–	–	0.025	–
Apechthis	–	–	–	0.005	0.050	0.045	–	–	–	0.027	0.11	0.12	0.20	0.19	–	0.16	0.053	0.033	0.40	0.014	0.006	0.47	0.076	–
Itoplectis	0.036	0.013	0.016	0.019	0.018	0.025	–	–	0.13	0.003	0.006	0.015	0.067	0.042	–	0.030	0.006	0.016	0.041	–	0.012	0.004	–	–
Phaeogenes	0.035	0.051	0.005	0.040	0.088	0.090	0.14	–	0.26	0.074	0.17	0.072	–	0.063	–	–	–	0.033	–	–	0.072	–	0.026	–
Psychophagus	–	–	0.047	0.048	1.3	0.14	–	–	–	–	0.20	–	–	0.032	–	0.004	–	0.012	0.026	–	0.034	0.14	0.17	–
Amblymerus	0.002	–	–	–	–	–	–	–	0.26	0.005	0.068	0.007	–	–	–	0.004	–	–	–	–	0.034	–	0.025	–
Total M/S Ratio	0.43	0.57	0.67	0.92	5.1	1.4	7.9	3.8	1.8	0.81	2.0	1.9	4.5	2.1	0.94	0.46	0.48	0.13	0.87	0.54	0.19	1.2	3.4	0.57
Per cent Mortality	30	36	40	48	84	58	89	79	65	45	67	65	82	68	48	31.4	32	11	47	34	16	55	77	36

Lac Seul Outbreak:

Parasite	Plot S1							Plot S2						Plot S3			Plot S4		
	1950	1951	1952	1953	1954	1955	1956	1950	1951	1952	1953	1954	1955	1952	1953	1954	1952	1953	1954
Apanteles	0.42	0.083	.14	.049	.23	.11	0.073	.25	.15	.078	.054	.046	0.064	.074	.014	.24	.062	.034	.087
Glypta	0.094	0.20	.30	.091	.19	.10	0.065	.097	.29	.26	.16	.22	0.19	.20	.16	.20	.26	.19	.23
Meteorus	0.007	0.004	.045	.048	.17	.036	3.3	.036	.011	.023	.011	.042	0.033	.005	.016	.003	.008	.010	.008
Lypha	0.013	0.003	.005	.010	.005	.006	–	.005	.006	.050	.023	.025	0.045	.005	0	.013	.008	.006	0
Omotoma	0.022	0.017	.004	–	.008	.024	0.008	.019	.015	.003	.005	.013	0.052	.021	.009	.004	.006	0	.010
Itoplectis	0.025	0.003	.004	.009	.025	.009	–	.029	.002	.010	.011	.007	0.17	0	0	.010	.013	.035	.010
Apechthis	0.002	0.001	–	.003	.060	.064	–	.002	.002	0	.022	.003	0.052	.005	.013	.022	0	.014	.021
Phaeogenes	0.023	0.020	–	.002	.16	.18	–	.009	.024	.028	0	.046	0.17	.14	.044	.034	.020	.011	.087
Total M/S Ratio	.60	0.34	0.46	0.25	1.0	0.86	4.0	0.48	0.46	0.46	0.310	0.43	0.99	0.53	0.28	.49	0.42	0.31	0.49
Per cent Mortality	37	25	31	20	50	46	80	32	31	32	24	30	50	35	22	33	29	24	33

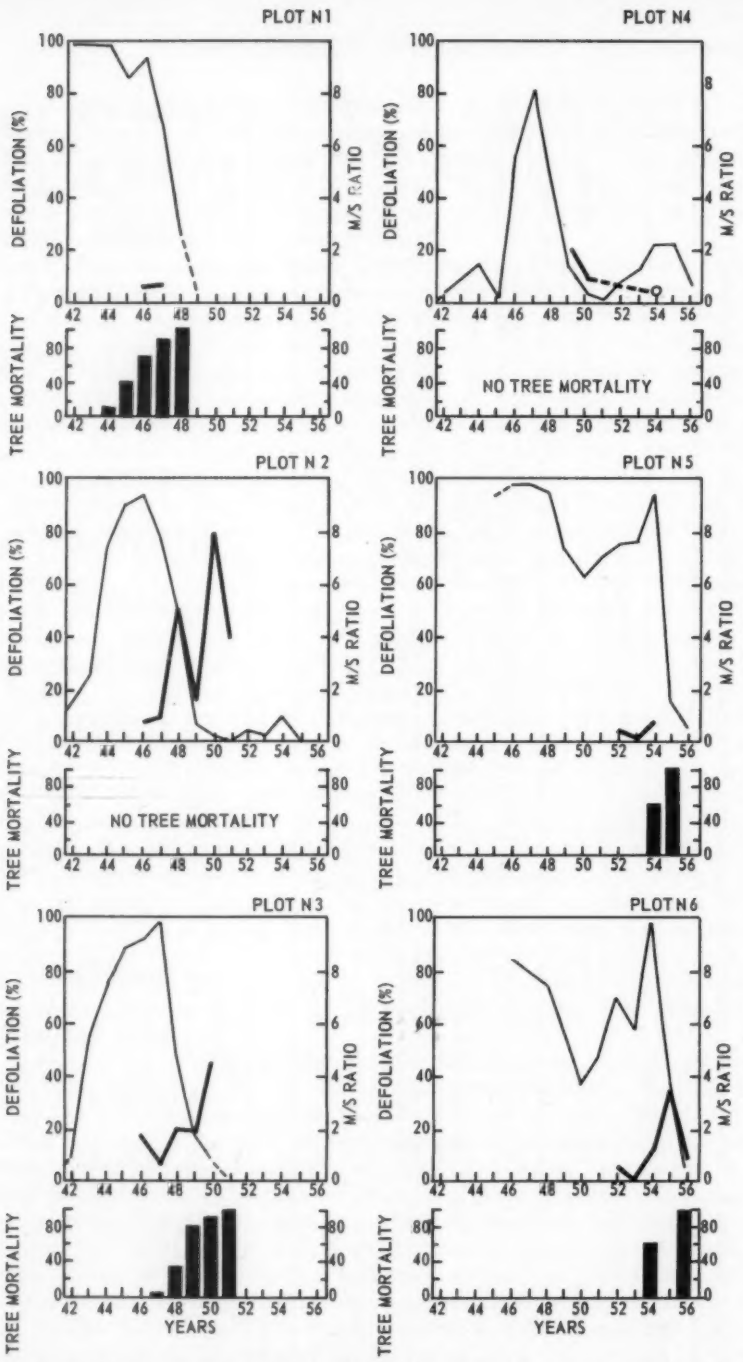

Fig. 2. Defoliation records and Mortality/Survival ratios for the six parasite study plots in the Nipigon outbreak.

Defoliation of the current year's growth
M/S Ratio

the population level closely paralleled conditions in Plot N3. However, the trend in M/S ratios was somewhat different. It was of the same order as for Plot N3 in 1949 but failed to rise sharply in 1950. *Meteorus*, though common, did not reach the high level of abundance recorded in the other plots studied that year. Rather, the M/S ratio declined as a result of a lower incidence of *Apanteles* and *Glypta* and the almost complete absence of pupal parasites in the small number of budworm pupae that could be obtained. The trees in the plot rapidly recovered and except for reduced ring growth in 1948-50 (3) now show no long-term effects of the outbreak. This rather different course of events undoubtedly resulted from the plot being located at the periphery of the outbreak. The budworm population level was never very high and both the host and the parasite populations were probably being maintained, at least in part, by an overflow from the main body of the infestation. The decided drop in budworm abundance in the main body of the infestation in 1949 could then be reflected in such border areas as Plot N4 without the continued local appearance of large numbers of parasites or other control factors.

In Plots N2 and N4 where no tree mortality occurred, defoliation increased appreciably in 1954-55 (Fig. 2). This general resurgence occurred throughout the Nipigon outbreak area and was particularly apparent on white spruce trees. Plots N5 and N6 provided information on parasites during this resurgence. These plots were selected in 1952 in balsam fir stands which although within the intermediate zone of the outbreak had not declined as rapidly as elsewhere. The budworm population level in this area declined in 1949 and 1950 but not to the same extent as in other parts of the outbreak; defoliation declined from values near 90 per cent to about 50 per cent. After 1950, defoliation progressively increased until by 1954 it was again in excess of 90 per cent. Foliage production during this period was exceedingly poor and the number of budworms required to produce near complete defoliation in 1954 was much less than in 1947-48 when the trees were more vigorous and foliage production normal. It was possible to obtain parasite records in Plot N5 until 1954; these resulted in some of the lowest M/S ratios obtained. The species responsible for the apparent uptrend in parasitism in 1954 were *Meteorus* and *Apechthis*. In Plot N6 the less severe defoliation history resulted in a slower decline of the stand and permitted parasite observations until 1956. The pattern in 1952-54 was nearly identical to that obtained for Plot N5. The uptrend in parasitism noted in 1954 continued and the M/S ratio for 1955 was higher because of further increases in *Meteorus* and new increases in *Psychophagus* and *Apechthis*. Tree mortality was almost complete by 1956 and only a small number of insects could be collected. The only parasites obtained were *Apanteles*, *Glypta*, and *Meteorus*, the latter being the most common.

Despite the limitations of M/S ratios, the above results indicate that they do reflect the conditions so as to show a general correlation with one measure of population trends — the defoliation record. On this basis it is possible to generalize on the role of insect parasites in the course of the Nipigon outbreak. More continuous records for certain of the plots would have greatly strengthened the opinions expressed below.

Parasites were not abundant and of little importance in the early stages of the outbreak (Plot N1, 1946-7) and the only limiting factor was food supply. While this limit was being reached and trees were dying at the epicentre, the outbreak was spreading out rapidly in all directions. Natural barriers, such as extensive stands of non-host trees, burned-over areas, and settlement, soon exerted

an influence on this spread. The maximum boundaries of severe infestation to the south, west, and north of Lake Nipigon were established very early restricting later spread to areas east of Lake Nipigon. Plots within the intermediate zone (Plots N2 and N3) show that the parasite complex underwent marked changes during the decline of the outbreak and that certain species became unusually abundant. Some evidence of the decline in the outbreak became apparent before the M/S ratios increased appreciably, indicating either that other mortality factor(s) became operative before the parasites or that the present methods do not adequately show the interrelationships at this critical point. In any event parasites generally, and *Meteorus, Lypha, Omotoma, Apechthis,* and *Psychophagus* in particular, had responded to the increased number of budworms and were an important factor in the dramatic virtual disappearance of the Nipigon outbreak in 1949-50. This collapse was sufficiently general that budworms disappeared from stands on the border of the outbreak (Plot N5) where an adequate food supply remained and parasites, though common, were not as abundant as in the intermediate areas. In restricted areas (Plots N5 and N6) the budworm population level showed a resurgence in 1954. Parasitism promptly increased and *Meteorus, Apechthis,* and *Psychophagus* again contributed, along with host tree mortality, to the final decline of the Nipigon outbreak.

Only a few species of parasites showed evidence of being able to function as "key factors" (26) during the collapse of the Nipigon outbreak. The methods employed may not be sufficiently sensitive to appreciate the smaller but perhaps meaningful variations in other parasites. The more apparent variations in the incidence of certain parasite species are discussed in the following paragraphs.

Apanteles fumiferanae Vier.

This parasite was essentially omnipresent in early larval collections and had the highest occurrence rating of any species (Table II). It was only lacking from Plot N5 in 1953 when parasite incidence was at the lowest level recorded during these studies. Although usually present in appreciable numbers, *Apanteles* showed no evidence of assuming an important role as a control factor. M/S values (Table IV) tended to decrease as the outbreak progressed. The only exception was a period of unusual abundance in Plot N2 in 1950-51. *Apanteles* did not demonstrate the variability required of a "key" mortality factor and, in fact, seemed to decline in importance as the outbreak progressed. Other authors (15, 19) have recorded much higher incidences of *Apanteles* and have attributed considerable importance to it.

Glypta fumiferanae (Vier.)

Like *Apanteles* this parasite is nearly always present in appreciable numbers. It was often the most common parasite, but again seemed to decline in numbers as the outbreak progressed. Except for a minor peak in Plot N2 in 1951 similar to *Apanteles,* this species showed only minor fluctuations in its steady downward trend.

Meteorus trachynotus Vier.

The most outstanding changes in the occurrence of any individual parasite species involved this braconid. In 1946 and 1947, it was relatively uncommon in all plots with its highest incidence in Plot N1 near the centre of the outbreak. A steady increase in the abundance of *Meteorus* followed until by 1949 in Plot N3 and by 1950 in Plot N2 parasitism had reached rather spectacular proportions (Table IV). Following this period of abundance *Meteorus,* like most other

parasites, became relatively uncommon in the limited amount of budworm material that could be obtained between 1952 and 1954. However, in the general resurgence of budworm numbers in 1954, *Meteorus* again became abundant in Plot N6 and undoubtedly contributed to the return of budworm numbers to a very low level in 1956. *Meteorus* appeared to be the most effective parasite in the Lake Nipigon outbreak as its incidence fluctuated considerably and reached levels not paralleled by other species.

The possible importance of *Meteorus* had not been recognized until pointed out by the senior author in 1948 (21). Although always listed as being present in appreciable numbers, it had attracted no particular attention. In 1950 Dowden and Carolin (16) noted that although its incidence did not approach the combined totals for *Apanteles* and *Glypta*, it did show a gradual increase in importance with the decline in the outbreak they were studying. Jaynes and Drooz (19) in presenting their data for studies in Maine also showed a gradually increasing abundance for *Meteorus* although again at levels much less than for *Apanteles* and *Glypta*. More recently striking increases in the occurrence of *Meteorus* during the final years of the budworm outbreak in northern New Brunswick and the Gaspe region of Quebec have been reported (8, 35).

Diptera

Although ten species of Diptera were reared from the spruce budworm in northwestern Ontario, only two occurred with sufficient regularity and in sufficient numbers to warrant individual comment. These were *Lypha setifacies* (West.) and *Omotoma fumiferanae* (Tot.). Both showed a slow but definite upward trend between 1946 and 1950. Following the general decline of the budworm outbreak, their occurrence became rather erratic. Neither these species nor the entire Diptera complex appear to have played more than a nominal role in the impact of parasites during the outbreak. An interesting site preference was apparent between *Lypha* and *Omotoma*. The former was more abundant in the mature stands (Plots N3 and N4) while *Omotoma* was more common in the reproduction stands (Plots N1 and N2).

Apechthis ontario (Cress.)

This parasite was of little consequence in the reproduction plots (N1 and N2) but showed a consistent upward trend in other plots. *Apechthis* reached considerable importance in Plot N3 in 1950 and was one of the few species to react during the resurgence period in 1954.

Itoplectis conquisitor (Say)

Itoplectis was recovered from most collections of spruce budworm pupae but it was only a minor element in the parasite complex. During the final years of the outbreak its incidence was very low, particularly in the reproduction Plots N1 and N2.

Phaeogenes hariolus (Cress.)

This parasite occurred regularly but showed very inconsistent and erratic trends. Generally speaking it showed no increase in importance as the outbreak progressed.

Chalcidoids

Two species of chalcid, *Amblymerus verditer* (Nort.) and *Psychophagus tortricis* (Brues), appeared with considerable regularity and presented the most enigmatic picture of any of the parasites. *A. verditer* was the least common of

the two and except for a peak in abundance in Plot N3 in 1946 was relatively unimportant. *A. verditer* was not found in Plot N2 where *P. tortricis* reached a very high level of abundance in 1948. Curiously, this was the only year in which *P. tortricis* was collected from Plot N3. This strong plot preference was not apparent in records from Plots N4, N5, and N6 where *P. tortricis* was the more abundant parasite. In fact, it reached a relatively high occurrence in Plot N6 during the period of resurgence in 1954-55. The complete absence of both species in certain years was as striking as their periods of short-lived abundance.

Some authors (15, 38) consider that both chalcids are characteristically secondary parasites on such species as *Itoplectis*, *Apechthis*, and *Phaeogenes*. It is improbable that this is their normal habit in northwestern Ontario. When the trend and magnitude of the possible primary parasites that could serve as hosts are compared with the occurrence of chalcids, it is illogical to consider that the chalcids are strictly secondary. When abundant the parasitism by chalcids often surpassed even the largest combined totals obtained for their potential primary hosts. At the same time these primary parasites showed no significant depressions in their occurrence. To support this indirect evidence over one hundred preserved pupae and budworm pupal cases that had given rise to chalcids were carefully dissected. Only one pupal skin and one preserved pupa contained evidence of a large hymenopterous parasite in addition to the polyembryonic chalcids.

The Lac Seul Outbreak

Parasite studies in the Lac Seul area were undertaken in 1950 as part of broader ecological studies of the spruce budworm. The four study plots used for various periods are shown in Fig. 1 along with the status of the Lac Seul outbreak in 1952 and 1958 (30). A summary of the stand composition, infestation history, period of study, and the eventual impact of the outbreak are outlined briefly for each plot in the following paragraphs.

Plot S1 was located approximately 14 miles from the centre of the outbreak in a mature balsam fir stand. Some white spruce and white birch trees were present and the site quality was fair. Parasite studies were begun in 1950 whereas spruce budworm defoliation had begun in 1945 and had been severe since 1947. The first tree mortality was observed in 1951 and all merchantable-sized balsam fir trees were dead by 1956 necessitating the abandonment of parasite studies.

Plot S2 was located 10 miles farther from the centre of the outbreak and was also in a mature balsam fir stand. The site quality was somewhat better than Plot S1 and the balsam fir trees were about 30 years older. A few overmature black spruce, jack pine, and trembling aspen trees were present in the stand. The first spruce budworm defoliation occurred in 1947, two years later than in Plot S1. In 1948 the trees were completely stripped of the current growth and very severe defoliation continued until 1956. Initial tree mortality was also delayed by two years in comparison with Plot S1; it began in 1952 and reached nearly 100 per cent of the merchantable stems by 1956. Parasite studies were conducted from 1950 until 1955.

Plots S3 and S4 were established in the immediate vicinity of Plot S2 and were located in a stand with an abundance of mature white spruce and young open-grown immature balsam fir trees. Parasite studies were maintained from 1952 to 1954 to provide a limited basis for comparison of the parasite complex under these different conditions. All balsam fir and a few white spruce trees in Plot S3 eventually died. None of the young balsam fir trees in Plot S4 were killed.

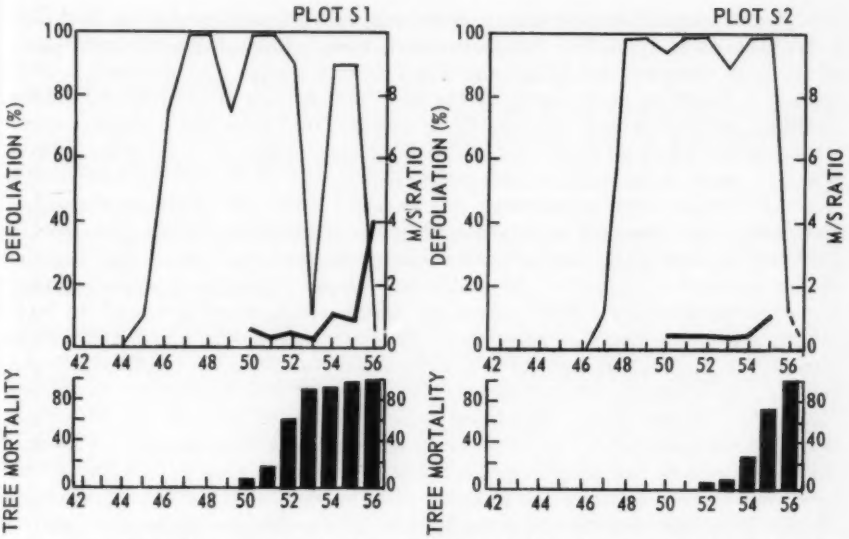

Fig. 3. Defoliation records and Mortality/Survival ratios for two parasite study plots in the Lac Seul outbreak.
Defoliation of the current year's growth
M/S Ratio

The Lac Seul plots provide a seven year comparison between two quite similar plots located near the centre of the outbreak but differing by approximately two years in their budworm history. Short-term comparisons are also possible with single plots located in the same general area but in an immature balsam fir stand and a white spruce stand. Although both the Nipigon and Lac Seul outbreaks began at approximately the same time, the latter did not decline after approximately 10 years as did the Nipigon outbreak. Rather, the Lac Seul outbreak has continued for a period of 20 years and no major change is expected in 1959 (30). The present data therefore only express the parasite conditions near the centre of the outbreak in the five- to six-year period immediately preceding the complete breakup of the stands in which the study plots were located. Unfortunately, the parasite study program could not be expanded to keep pace with the Lac Seul outbreak and except for some extensive Forest Insect Survey records little is known of parasite conditions in the present active outbreak areas.

The amount and distribution of spruce budworm material reared from the Lac Seul plots is shown in Table III and the species of parasite obtained are included in Table II which has already been discussed in some detail. The analytical technique described above was applied to the data and the M/S ratios obtained for the more common parasites and for the plots as a whole are shown in Table IV. The defoliation histories for Plots S1 and S2 are included in Fig. 3 to show the possible significance of changes in the M/S ratios. Unlike the Nipigon records shown in Fig. 2 the Lac Seul defoliation records were obtained by classifying the sample branches into broad categories as follows: 10, 25, 50, 75, 90, 95, and 100 per cent defoliation. Records are not available for Plots S3 and S4. The observations that can be drawn from Table IV and Fig. 3 are discussed for the individual plots in the following paragraphs.

Plot S1 located just beyond one of the original epicentres of the Lac Seul outbreak showed no budworm defoliation until 1945. There followed seven years of severe to complete defoliation and when parasite studies were initiated in 1950 some tree mortality had already occurred. The striking decline in defoliation in 1953 resulted from very unusual spring weather conditions which besides having a pronounced effect on the spruce budworm in some locations had a more general effect on other early season forest insects such as the forest tent caterpillar (7). The M/S ratios were consistently low between 1950 and 1953 but showed a decreasing trend from the unusual abundance of *Apanteles* in 1950. The ratio in 1953 was approximately one-half the value of the previous year largely because of the reduced incidence of *Apanteles* and *Glypta*. This may possibly reflect the disproportionately adverse effect the severe spring conditions had on budworms containing these parasites that overwinter within the host. Defoliation returned to its previous high level in 1954 as did the incidence of *Apanteles* and *Glypta*. In addition, marked increases in *Meteorus* and *Phaeogenes* raised the M/S ratio to a new high. There was a slight decline in 1955 but the M/S ratio moved ahead considerably in 1956 due to an abundance of *Meteorus*. Although the appearance of this parasite coincided with a marked drop in defoliation, the latter was more a result of the complete deterioration of the stand. Essentially all trees of a merchantable size were dead by 1955 and spruce budworm material could only be collected with extreme difficulty in 1956. The sequence of events at this plot closely parallels those at Plot N3. However, there were important differences. The period of defoliation that preceded the complete breakup of the stand was much longer and more intense in Plot S1. Most significant is the fact that the marked increase in the M/S ratio did not coincide with or closely follow a general collapse throughout the Lac Seul outbreak. It did occur, however, at the same relative point of time in the sequence of events at the two plots.

In Plot S2 severe defoliation began in 1947, two years later than in Plot S1 and showed only a minor decline after the poor spring of 1953. Tree mortality first occurred in 1952, again two years later than in Plot S1, and proceeded very rapidly until essentially complete in 1956, only one year later than in Plot S1. The M/S ratios were also very similar to Plot S1 except that the tendency to increase appreciably was delayed until 1955. The only parasite species showing this tendency were some of the pupal parasites, particularly *Phaeogenes*. *Meteorus* increased slightly in 1954 but declined in 1955. Unfortunately, spruce budworm material could not be collected in 1956 and whether *Meteorus* became as abundant as it was in Plot S1 in 1956 is not known. In general, however, the two plots were very similar, the major difference being the initial appearance of spruce budworm outbreak conditions.

The parasite complex from collections from white spruce trees in Plot S3 showed no major qualitative differences from the balsam fir plots and a comparison of the M/S ratios in Table IV indicates few if any differences in the relative occurrence of the more common parasites. The only trends apparent are the large number of *Apanteles* recorded in 1954 and the general low level of *Meteorus*.

The results from the immature balsam fir stand of Plot S4 showed both similarities and differences with results from Plots S2 and S3. However, all three plots gave grossly similar results and the short period of observation prevents any definite conclusions.

The status of some of the parasites in the Lac Seul outbreak and comparisons with Nipigon conditions require comment.

Apanteles fumiferanae Vier.

This species showed the same general pattern as was evident in the Nipigon studies. It was always present and in good numbers early in the outbreak but gradually decreased in relative abundance.

Glypta fumiferanae (Vier.)

The trends for this parasite were very similar to *Apanteles*. It was always present and usually the most abundant parasite but showed little change during the course of the outbreak.

Meteorus trachynotus Vier.

This parasite was much less abundant than in the Nipigon plots. However, in plot S1 it increased in apparent importance as the outbreak progressed and in 1956 was comparable in occurrence to the conditions already reported for the Nipigon plots. In contrast, no comparable increase was recorded in the other study plots.

Diptera

The dipterous complex was somewhat smaller in the Lac Seul plots and the minor species had a much lower occurrence rating than in the Nipigon plots (Table II). This trend was also evident in the common dipterous parasites, *Lypha* and *Omotoma*. They were obtained in much smaller numbers than in the Nipigon rearings. The generally lower level of the M/S ratios for the Lac Seul outbreak is to a considerable degree the result of the much lower incidence of dipterous parasites.

Itoplectis conquisitor (Say)

The erratic occurrence of this pupal parasite was very similar to that obtained in the Nipigon studies.

Apechthis ontario (Cress.)

The results obtained for this parasite from the two outbreak areas were generally similar but no opportunity was provided to see if marked increases would occur in the Lac Seul outbreak similar to the Nipigon plots after the general collapse of the outbreak.

Phaeogenes hariolus (Cress.)

This species showed a consistent increasing trend in the Lac Seul plots instead of the erratic picture obtained in the Nipigon plots.

Chalcidoids

These polyembryonic parasites were not abundant in the Lac Seul plots. *P. tortricis* occurred only rarely while *A. verditer* was the most common. This agrees closely with the Nipigon results where *A. verditer* was recovered in great numbers from mature stands similar to Plots S1 and S2.

General Discussion and Conclusions

The present studies in northwestern Ontario bring the recorded total of parasite species that attack the spruce budworm to approximately 92. All major taxonomic groups of parasites are well represented and the egg, larval, and pupal stages are all affected. Hyperparasites are not uncommon but do not appear to

be a limiting factor for any parasite. Where the spruce budworm parasite complex has been studied in detail the important elements have consisted of the same 12 to 15 species. The less common and the occasional species vary considerably from region to region in both number and abundance. The present studies show that such differences occurred even between two contemporary outbreaks in northwestern Ontario. A total of 30 species were obtained of which 21 were common to both areas, four were found only in the Nipigon plots, and five only in the Lac Seul plots.

Of greater possible significance are variations in occurrence within and between plots from year to year. The ratings in Table II divided the parasite complex into three groups. The first were parasites almost invariably present and showing plot or yearly differences only in their relative abundance. The remaining groups contain examples of species showing strong regional or plot preferences (many of the Diptera and the chalcids) and examples of species which seem to reflect in their appearance certain periods of the outbreak sequence (e.g. species of *Horogenes*, *Eubadizon* and *Synetaeris*).

Only a few of the parasites appear sufficiently variable in their occurrence to play an important role in the spruce budworm control beyond the rather constant mortality caused by the complex as a whole. The species which best demonstrates this potential is *Meteorus*. However, the history of present and past outbreaks in Canada shows that parasites in combination with the other natural controls unfortunately do not become operative until large areas of balsam fir forest have been killed.

The extensive tree mortality that has occurred in both the Nipigon and Lac Seul outbreaks is ample testimony of the ineffectiveness of parasites and other natural controls. Once the required combination of a susceptible forest and a suitable climatic sequence (36) has triggered an outbreak, spruce budworm numbers rapidly outstrip control factors that react to increased host density. At or near the epicentre (Plot N1), all balsam fir trees and most white spruce trees are eventually killed by the repeated defoliation. Throughout a broad area surrounding the epicentre balsam fir trees in young open stands (Plot N2) or forming a very small component of mixed stands, may survive with only a loss of increment. However, the great majority are killed as well as many white spruce trees. The fate of individual balsam stands is a complex function of the distance from the epicentre (i.e. years of severe defoliation), tree age and vigour, and stand composition and structure. Within this outbreak zone the food supply becomes the prime limiting factor. However, certain parasites do show gradual or marked increases (Plots N3 and S1) that appear to hasten the rapid and complete collapse of the budworm population. In the Nipigon outbreak this rapid decline occurred simultaneously throughout the entire outbreak area including a large peripheral zone wherein severe defoliation had occurred for only one or two years. In this zone (Plot N4 and large areas east of Lake Nipigon) the budworm population dropped to near-endemic levels despite an adequate food supply. The affected stands have recovered and now show little effect of the outbreak. At the time of collapse parasites were considerably more abundant in these peripheral areas than they were at the epicentre early in the outbreak and, therefore, must be considered one of the factors contributing to the overall decline of the outbreak. The minor resurgence in budworm numbers in surviving peripheral or sprayed stands was accompanied by a prompt response in parasite numbers.

It is interesting to compare the Lac Seul and Nipigon outbreaks in the light of the above generalized comments. Although the pattern of activities near the

epicentre of both outbreaks was similar, the parasite increases in the Lac Seul plots did not coincide with a general collapse as in the Nipigon outbreak. The observed increases could be accounted for by the reduced number of hosts present following severe tree mortality. The reasons for this major disparity between the two outbreaks cannot be deduced from the data obtained in the present studies. However, one might postulate that the difference is only one of time and that a general collapse of the Lac Seul outbreak may yet occur. This is unlikely as it now covers a wide diversified area stretching from Lake Winnipeg nearly to Fort William and far south into Minnesota. The range of conditions that normally exist over this vast area could hardly result in the entire outbreak reacting as a unit. The abnormal spring conditions in 1958 and their severe effect on the spruce budworm in southeastern Manitoba (28) contrast sharply with the continued extension of outbreak conditions west of Fort William (30).

A more plausible explanation may lie in the quite different forests of the two regions. The Nipigon outbreak originated in Halliday's (18) Nipigon Section of the Boreal Forest and at its maximum extent completely covered this section as well as parts of the adjacent sections, particularly the Superior Section. The affected forests were relatively homogeneous and contained extensive stands of mature balsam fir. In contrast, the Lac Seul outbreak originated in the Western Transition Section. After remaining rather static until 1950 the outbreak spread extensively involving the English River Section and now covers the entire Quetico Section of the Great Lakes-St. Lawrence Forest. Forests in these Sections are quite varied and contain a high proportion of different species of pines and deciduous trees. Balsam fir is common but represented primarily by relatively small fragmented stands, often of young vigorous trees. The extensive outbreaks that occurred in the central transition zone of Ontario in the late thirties and early forties (14, 34) ran a similar course in similar diversified forests. The role of parasites under these circumstances is uncertain. It is most significant, however, that the incidence of parasitism in the Lac Seul study plots was consistently and appreciably lower than in the Nipigon plots. The average percentage of parasitism (Table IV) for the Nipigon plots was 52 per cent while the Lac Seul average was only 35 per cent. The quantitative difference and such gross qualitative differences as are evident in the Diptera complex lead to the conclusion that parasites were more important in the Nipigon outbreak and that their relatively lower incidence may be one of the factors contributing to the present status of the Lac Seul outbreak. The biological explanation of these differences poses many difficult but challenging problems, particularly in view of the importance attached to parasites in spruce budworm outbreaks in the mixed and discontinuous balsam stands of the northeastern United States (15, 19).

The limitations of the present experimental approach toward an appreciation of the role of insect parasites in the population dynamics of the spruce budworm are abundantly clear and serve to emphasize the need for a more comprehensive approach to the subject. The present data do show interesting gross trends which point to at least certain parasites functioning as important control factors. A more careful elucidation of these interrelationships can only be expected from the type of approach being followed by Morris (27) and his co-workers. Any precision they may add will not alter the fact that extensive tree mortality is a normal consequence of spruce budworm outbreaks in eastern Canada. Attempts to introduce new parasites into an already large and varied complex have not been successful and forest industries have, with some success, taken recourse to large-scale applications of insecticides (2). Control through forest management has

frequently been recommended but has yet to be adequately demonstrated. A knowledge of the detailed requirements of the more important parasites could well form a profitable part of such investigations.

Acknowledgments

The scope of the present studies would not have been possible but for the assistance and co-operation of many persons. Most important were those who continued the field studies and preliminary analysis on a maintenance basis after 1950 in the Nipigon area and after 1954 in the Lac Seul area. S. McDonald and G. Stairs were responsible for the Nipigon work and E. Smereka the Lac Seul work while K. R. Elliott co-ordinated the combined efforts in 1955 and 1956. The authors wish to extend their sincere thanks to these officers for their efforts and the privilege of using the information contained in their laboratory reports.

The manuscript was read by M. L. Prebble and R. M. Belyea and their comments have resulted in a number of improvements. Officers of the Hymenoptera and Diptera sections of the Entomology Research Institute provided many parasite determinations and reviewed the taxonomic terminology used throughout the paper.

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Some Humidity and Light Reactions of the Granary Weevil, *Sitophilus granarius* (L.) (Coleoptera: Curculionidae)[1]

By E. P. Smereka[2] and A. C. Hodson[3]

Introduction

The behaviour to moisture of a number of stored-product insects; *Tenebrio molitor* (Pielou and Gunn, 1940), *Ptinus tectus* (Bentley, 1944), *Tribolium castaneum* (Willis and Roth, 1950) and *Tribolium confusum* (Roth and Willis, 1951) have been studied. All these species live in a dry environment in flour and all have shown a preference for the drier of any two humidity alternatives. The moisture reactions of the granary weevil were studied since this species develops in a relatively moist environment (Richards, 1947) and should show a contrast to the reactions of the above species. The supplementary studies of this investigation were to determine the effect of moisture conditioning on the moisture reactions and to study the interaction between light and moisture.

The experimental techniques were developed at the University of Minnesota, but most of the experimental work was done at the Forest Insect Laboratory, Sault Ste. Marie, Ontario.

Material and Methods

Two types of apparatus have been designed with the same principle in mind; that of offering experimental animals a choice of any combination of two humidities. A relatively complex apparatus called an olfactometer was designed by Willis and Roth (1950), but a simpler alternative chamber, Fig. 1, similar to that constructed by Gunn and Kennedy (1936) was found suitable for this study.

An evaporimeter, consisting of a glass tube of very small bore, such as a thermometer with both ends cut off, was used to measure moisture differences. It was essentially similar to one described by Wellington (1949), but cigarette- rather than filter-paper was used to increase the evaporation area. The evaporimeter was calibrated by noting the time taken to evaporate 0.66 cu. mm. of water over standard sulphuric-acid solutions (Solomon, 1951). The time required was less than two minutes at lower humidities and up to 30 minutes at higher humidities. The determinations, which were fairly uniform but increasingly variable at higher humidities, were used to make the curves in Fig. 2, from which evaporation time was converted to relative humidity. The data for the curve at 27° C. were obtained at Minnesota, but facilities at Sault Ste. Marie were available only at 21° C. and another curve was made. The evaporation rate at 21° C. and 0 per cent relative humidity was 0.39 cu. mm. per minute and 0.05 cu. mm. per minute at 90 per cent relative humidity.

Evaporation rates in the alternative chambers were taken just before and after an experiment was conducted. No change occurred during that period. The actual humidity difference in the alternative chamber was somewhat different from the stated difference. With differences of 30, 20, and 10 per cent, the actual differences obtained were approximately 15, 10, and six per cent, respectively. However, to facilitate discussion and interpretation of data, only standard (equivalent to relative humidities obtained over one sulphuric-acid solution) humidities and humidity differences will be used. The term per cent relative humidity will be abbreviated to R. H., e.g., 90 per cent relative humidity will be designated as 90 R. H.

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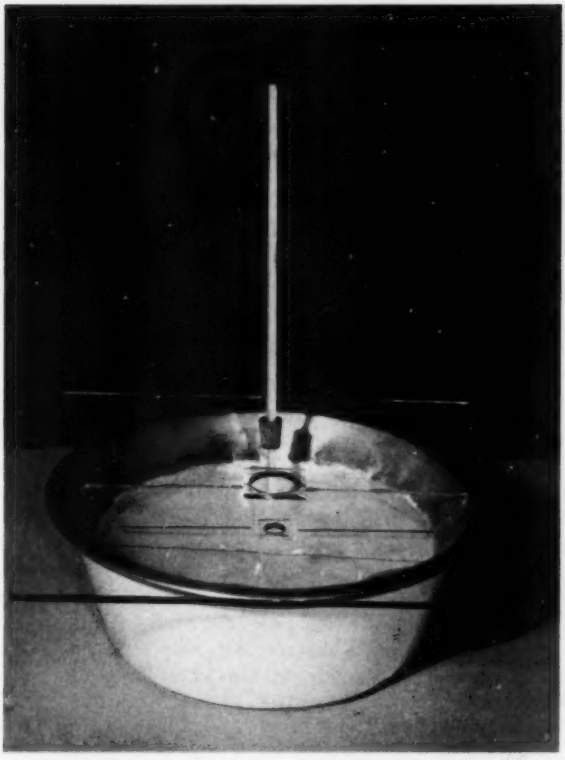

Fig. 1. A photograph of an alternative chamber showing evaporimeter in position.

The beetle cultures were maintained in No. 3 Manitoba northern wheat at 21 ± 1.0° C., between 65 and 75 R. H., and were given approximately eight hours of darkness in 24. Both beetles and wheat were obtained from the Stored Products Laboratory, Canada Department of Agriculture, at Winnipeg.

An entire culture of two- to four-week-old beetles was thoroughly sifted before selecting experimental animals. Immediately after sifting, most beetles were apparently photonegative, and from this group active beetles were randomly selected. The selected beetles were confined in groups of 25 in petri plates with nylon-tulle covers, and conditioned for 12 hours at either 0, 75, or 100 R. H. in desiccators with the appropriate sulphuric-acid solutions. The temperature was maintained at 21 ± 1.0° C. and illumination was constant in the experimental area.

Twelve chambers each with 25 beetles were used; four were controls and eight were alternative chambers. The zone of sharpest gradient, set as an area two centimeters wide about the mid-line, was designated as the nonreactive zone and beetles in this zone were considered nonresponsive. After the beetles were introduced into the alternative chamber, counts were made in the wet, dry, and nonreactive zones at five, 10, 20, and 30 minutes and thereafter at 15-minute intervals until the end of the second hour. From the sixth to the 24th hour, 10 counts at least an hour apart were made. Ten counts were made at least an hour apart during the second 24-hour period of the few experiments carried

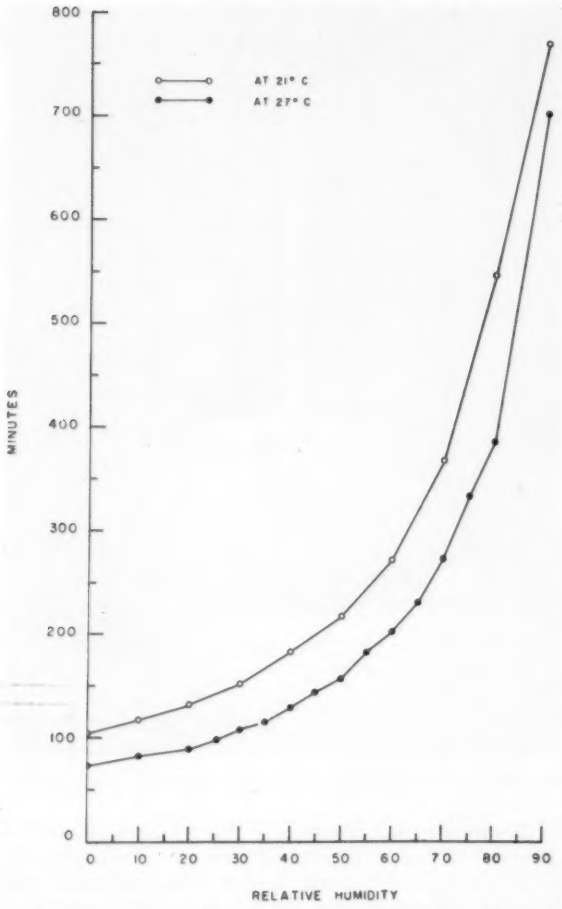

Fig. 2. Time required to evaporate 0.66 mm.^{3} of water over standard sulphuric acid solutions.

through to the 48th hour. Similar counts were also made in the control chambers, the humidity of which was always the same as the lowest alternative of any particular experiment.

Orientation experiments were carried out in small petri plates, which could be divided in two when necessary by glass partitions sealed with paraffin. Tracking to a point source of humidity was done in an alternative chamber.

A study of the interaction between light and humidity was carried out in conjunction with the humidity-reaction experiments. At the end of the second hour of the humidity experiments, either the dry or the wet side of each chamber was covered with black paper. Beetles were counted in each zone after five, 15, 30, and 45 minutes; then the paper was reversed and two more counts were made after five and 15 minutes. The difference in light intensity between covered and uncovered portions of the chamber was not determined.

Temperature reversal studies were carried out in a room maintained at 5.5°C. The half-darkened chamber with 25 beetles was maintained at 20° C.

with a hot-plate for two to three hours before the temperature was reduced. By turning off the hot-plate, a temperature drop of 1.0° C. every seven to eight minutes was obtained. Reversal at the higher end of the temperature scale was carried out by turning up the hot plate so a temperature rise of 1.0° C. per minute was obtained.

As a means of assessing intensities of reaction an index, $\frac{W - D \times 100}{N}$, was used, where D and W are, respectively, the number of beetles in the dry and wet side of the alternative chambers and N is the total number of beetles. This index takes into account those beetles that are in the nonreactive zones and was used by Bentley (1944) and Willis and Roth (1950). It ranges in values from +100 to −100 and zero implies no reaction. A similar index was used in the light experiments, but L was substituted for W and represented the number of bettles in the light and D represented the number of insects in the dark side.

Results

Locomotor Activity

To obtain some quantitative data on the effect of relative humidity on locomotor activity, three replicates were set up at each of the following humidities: 0, 30, 60, and 100. Ten chambers (petri plates sealed edge to edge), each containing five beetles, constituted a replicate. At 0 R.H. approximately 75 per cent of the beetles were active, but after 48 hours the per cent activity started decreasing, probably because of death by desiccation. However, it was impossible to differentiate between dead and inactive beetles without opening the chamber, so if a beetle was dead, it was classified as inactive. Activity at 30 and 60 R. H. appeared to be greater than at 0 R. H., and an appreciable decrease in activity did not occur until the 80th hour at 30 R. H. and the 120th hour at 60 R. H. This decrease is also attributed to death by desiccation, especially for the beetles at 30 R.H., and certainly not to starvation, since beetles were still active at 100 R. H. (assuming no marked increase in metabolic rate at lower humidities (Edney, 1957)). At 100 R. H. the per cent of beetles active was appreciably lower than at the other three humidities, but remained fairly constant to the 144th hour, and some beetles were still active after two weeks. *Ptinus tectus* gave the opposite results, i.e., the beetles were more active in moist air, but after 10 to 12 days desiccation they were more active in dry air (Bentley, 19444).

Humidity Reactions

Fig. 3 shows the results obtained with relative-humidity alternatives of 100 and 75 (Fig. A), 75 and 45 (Fig. B), and 45 and 15 (Fig. C). The effect of both conditioning and position on the humidity scale is clearly shown in these figures. When the alternatives were 100 and 75 R. H., beetles conditioned at 0 R. H. gave a wet reaction throughout the course of the experiment. Beetles conditioned at 100 R. H. were negative for the first two hours and then gradually became as strongly positive as the ones conditioned at 0 R. H. Alternatives of 75 and 45 R. H. produced a strong positive reaction if the beetles were conditioned at 0 R. H. Beetles conditioned at 100 R. H. were unreactive for the first two hours and became positive more rapidly than those in the 100 to 75 R. H. gradient. When the alternatives were 45 and 15 R. H. beetles conditioned at 0 R. H. did not react as strongly positive throughout the experiment as those above. Beetles conditioned at 100 R. H. were only slightly reactive, negatively for the first five hours and positively after the sixth hour. Beetles conditioned

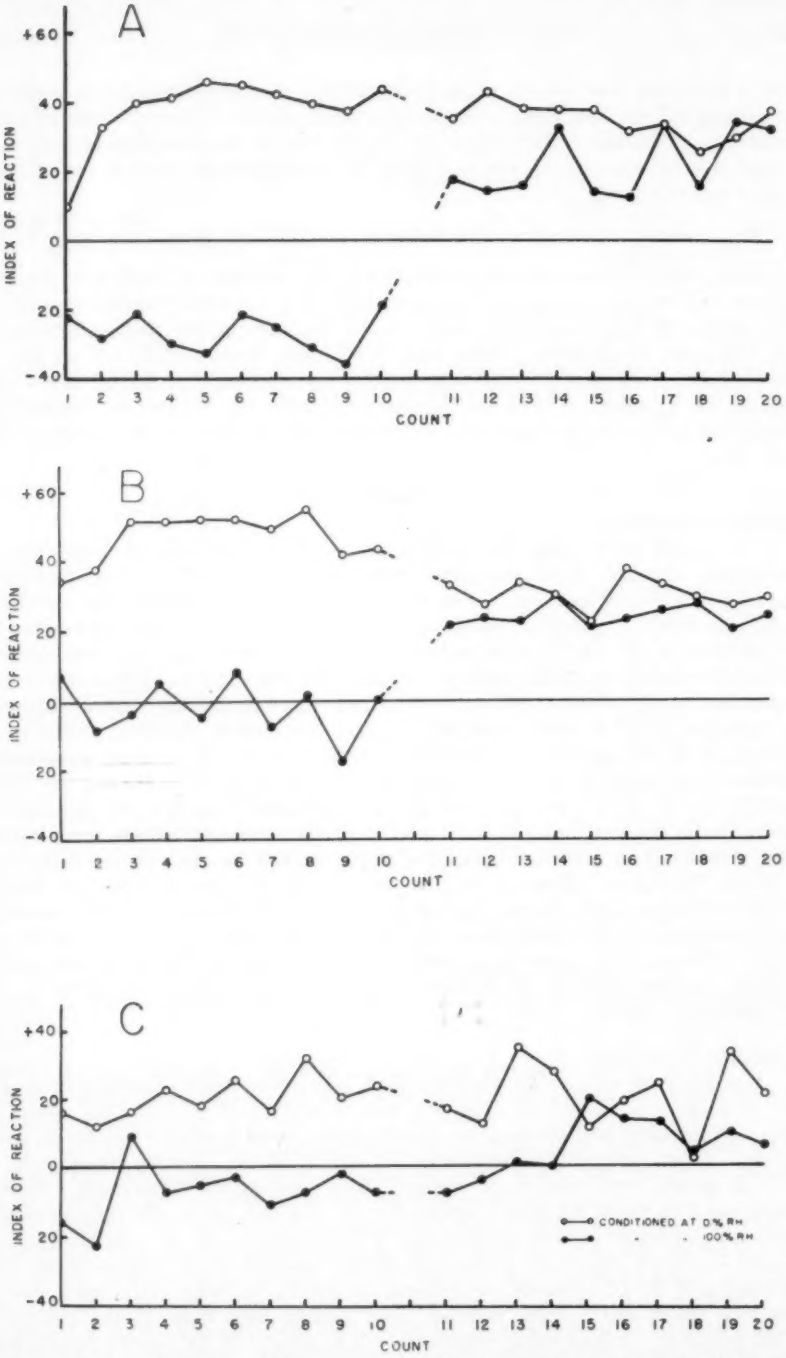

Fig. 3. Index of reaction of beetles conditioned at 0 and 100 R. H. at various humidity alternatives; A. 100-75 R. H., B. 75-45 R. H., C. 45-15 R. H. The first four counts were made after five, 10, 20 and 30 minutes; counts five to 10 at 15-minute intervals; and counts 11 to 20 were made at intervals of one hour or more.

TABLE I.

Chi-square comparisons of total number of beetles in the control and alternative chambers at various relative humidity alternatives during the first two hours and the second to the twenty-fourth hours.

Relative Humidity Alternatives	Conditioning	Hours 0–2	Direction of Reaction	Hours 2–24	Direction of Reaction
0–30	0	**	Wet	**	Wet
	75	—		—	
	100	—		—	
15–45	0	**	Wet	**	Wet
	100	—		—	
30–60	0	**	Wet	**	Wet
	75	—		—	
	100	—		**	Wet
45–75	0	**	Wet	**	Wet
	100	—		**	Wet
60–100	0	**	Wet	**	Wet
	75	**	Wet	**	Wet
	100	*	Dry	—	
75–100	0	**	Wet	**	Wet
	100	**	Dry	**	Wet
0–20	0	—		—	
	100	—		—	
20–40	0	*	Dry	—	
	100	—		—	
40–60	0	**	Wet	**	Wet
	75	—		—	
	100	—		—	
60–80	0	**	Wet	**	Wet
	100	—		*	Wet
80–100	0	**	Wet	**	Wet
	75	—		—	
	100	—		—	
40–50	0	—		—	
	100	—		—	
50–60	0	*	Wet	—	
	75	—		—	
	100	—		—	
60–70	0	—		**	Wet
	100	—		—	
90–100	0	**	Wet	**	Wet
	75	—		—	
	100	**	Dry	—	

*Significant at 95%.
**Significant at 99%.

at 75 R. H. were considered "normal" and gave only slightly positive humidity reactions. They did not react at the dry end of the humidity scale, and did not react at the moist end unless the humidity gradient was 30 R. H. or greater.

Experiments with alternatives of 100 and 60, 60 and 30, and 30 and 0 R. H. gave results similar to those of Fig. 3. Experiments were also conducted with humidity gradients of 10 and 20 per cent throughout the humidity range. Table I

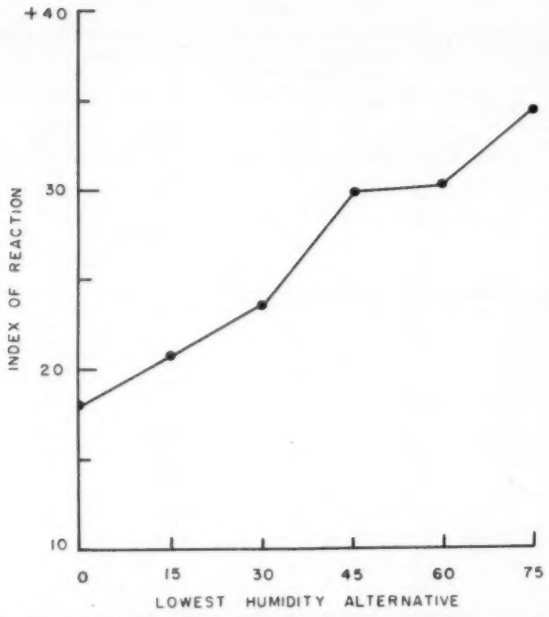

Fig. 4. Relationship of index of reaction to the lowest humidity alternative with a gradient of 30 per cent (the humidity gradient for the last point was only 25 per cent).

shows the chi-square comparisons of experimental and control results of all the humidity alternatives used. It can readily be seen that beetles conditioned at 0 R. H. react positively throughout the humidity range, providing that the gradient is steep enough. When the humidity gradient was 20 or 10 per cent, no reaction occurred unless one of the alternatives was, respectively, 20 R. H. or higher, or 60 R.H. or higher. A gradient of five per cent produced no reaction. Beetles conditioned at 100 R. H. did not give an initial negative reaction unless the lowest alternative was 60 R. H. or higher. However, a positive reaction was obtained after several hours if the lowest alternative was 30 R. H. or higher and the gradient was 30 per cent. If the gradient was only 20 per cent, a positive reaction was not obtained unless the lowest alternative was 60 R. H. or higher.

Fig. 4 shows the effect of lowest humidity alternative upon the intensity of the gradient, but also on the specific humidities at which the reaction is increased as either the lowest or highest humidity alternative increased. Thus, the intensity of reaction of the granary weevil depends not only on the steepness of the gradient. but also on the specific humidities at which the reaction is taking place.

Humidity Orientation

Humidity orientation was studied by tracking and observing single beetles at specific humidities and in humidity gradients. Each of 100 beetles was tracked for 15 minutes, 50 at 0 R. H. and 50 at 100 R. H. They were exposed in tracking chambers made of small petri plates for approximately three hours before observations were made and recorded. The sex of each beetle was

TABLE II.

Average distance (inches) moved by male and female beetles at 0 and 100 R. H.

Relative Humidity		Male	Female	Combined
	Number	24	26	50
0	Mean distance moved (ins.)	29.3	28.5	28.9
	Number	24	26	50
100	Mean distance moved (ins.)	17.7	20.6	19.2

determined by Richards' (1947) method, and the length of each track measured with a map measurer. The results shown in Table II illustrate hygrokinesis (Fraenkel and Gunn, 1940) since the beetles moved a longer distance in a given time at 0 R. H.

Individual beetles were also tracked in a huimidity gradient. Fig. 5a shows the typical tracks of a bettle conditioned at 100 R. H., and Fig. 5b of a beetle conditioned at 0 R. H., 15 minutes after introduction into alternatives of 30 and 60 R. H. Beetles conditioned at 0 R. H. moved much more than the ones conditioned at 100 R. H., and both showed more turning in the steep part of the gradient, illustrating both hygrokinesis and klinokinesis (Fraenkel and Gunn, 1940). Fig. 5c shows typical tracks of a beetle reacting to a point source (100 R. H.) of humidity that was produced by the introduction of an evaporimeter into an alternative chamber. The beetles appeared to move more rapidly and the number of turns increased as the distance from the humidity source increased.

Light Reactions

When one side of an alternative chamber was darkened, an interaction occurred between relative humidity and light if the humidity difference was large enough and at the high end of the humidity scale. A typical example, shown in Fig. 6, occurred when beetles conditioned at 0 R. H. were introduced into a 75-100 R. H. gradient. Curve A was obtained when the wet side was in the light, curve C when the dry side was in light, and curve B was the light reaction of the controls at 75 R. H. The data (totals) for these curves were statistically (by chi square) different. Table III gives the chi-square comparisons of all the experiments. Since the light intensity was not varied, the interactions were influenced only by those factors which influenced the humidity reactions, i.e., the humidity differences and the position of the alternatives on the humidity scale.

Experiments were also carried out on the effect of relative humidity and group size on the speed of development of the light reaction. Fig. 7 shows the effect of relative humidity. Groups of 25 beetles became photopositive after 30 minutes at 0 R. H., but took approximately two hours at 100 R. H. Since beetles moved faster at 0 R. H. than at 100 R. H., it appeared that speed of movement might have some effect on the length of time necessary for the groups to become photopositive. Although orientation to light was not studied, it appeared that photokinesis played a part in determining numbers on the light or dark side of a chamber. The effect of group size on the speed of development of the light reaction at 0 R. H. is illustrated in Fig. 8. Groups of 25 beetles became photopositive in 30 minutes, but groups of 400 beetles remained

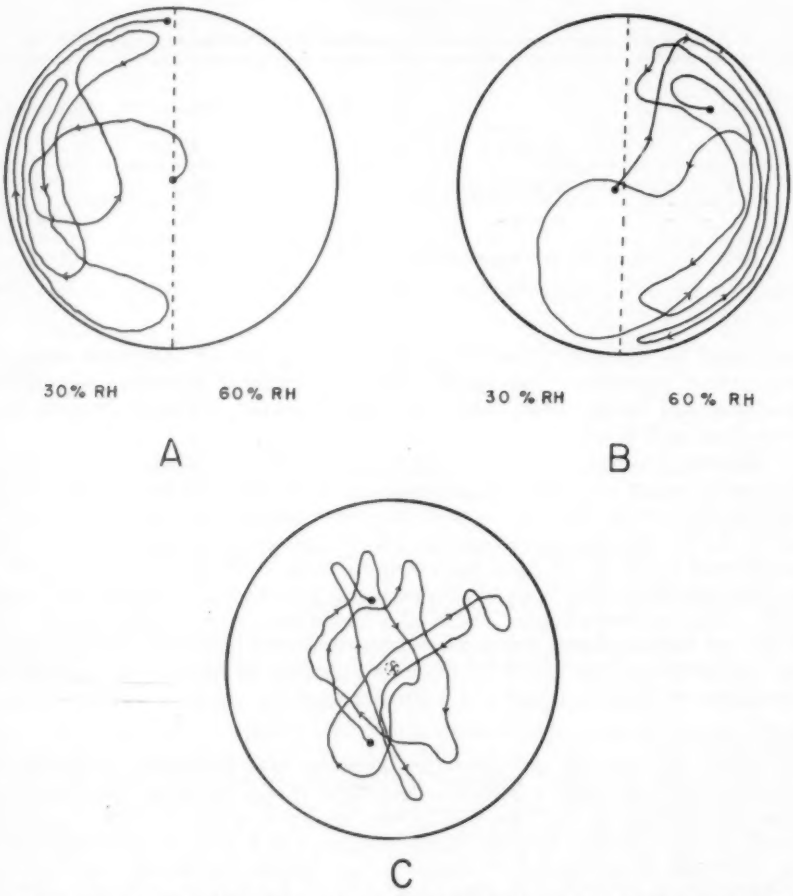

Fig. 5. Tracks of individual beetles; A conditioned at 100 R. H., B conditioned at 0 R. H. and C tracks to a point source (x in center of diagram) of humidity. A and B are five-minute tracks. C is a two-minute track.

photonegative for 30 minutes, then gradually became photopositive, and after three hours were as photopositive as the groups of 25. Groups of 100 and 200 took respectively 1.25 and two hours to become photopositive.

Reversal of the Light Reaction by Temperature

A reversal of the positive light reaction occurred between 11 and 7.0° C. at 0 R. H. At 9.0° C. and lower, 75 per cent or more of the beetles were photonegative. Above 20° C. and at 0 R. H., the beetles became increasingly active and increasingly photopositive, and 90 per cent were photopositive above 30° C. There was some indication of a reversal at 28 to 30° C. at 100 R. H., but excessive condensation prevented more exact observation. Beetles' reaction at the light-dark boundary was quite varied. Most beetles were indifferent to it, some followed along its path for a distance before proceeding into a zone, and a few strongly avoided crossing into the opposite zone.

TABLE III.

Chi-square comparisons of total number of beetles in the alternative and control chambers during the second and twenty-fourth hour when one side of the chamber was in darkness.

Relative Humidity Alternatives	Conditioned at 0				Conditioned at 100			
	Dry side in Light		Wet side in Light		Dry side in Light		Wet side in Light	
	2nd	24th	2nd	24th	2nd	24th	2nd	24th
40–50	—	—	—	—	—	—	—	—
50–60	—	—	—	—	—	—	—	—
60–70	**	**	—	—	*	—	—	—
90–100	**	**	*	*	—	**	*	*
0–20	—	—	—	—	—	—	—	—
20–40	**	—	—	—	—	—	—	—
40–60	—	**	—	—	—	**	—	—
60–80	**	**	**	**	—	**	—	—
80–100	**	**	—	—	—	—	—	—
0–30	—	—	—	—	—	—	—	—
15–45	**	—	**	**	—	**	—	—
30–60	**	—	—	—	—	**	—	—
45–75	**	**	**	—	—	—	—	**
60–100	**	**	**	—	—	**	—	**
75–100	**	**	**	**	—	**	—	—

*Significant at 95%.
**Significant at 99%.

Discussion

Although the data on humidity reactions showed clear, definite results, there was a good deal of variability in response, especially when the experiments were conducted at the dry end of the humidity scale and/or with a small humidity gradient. S. *granarius* appeared to differ from other stored product insects by showing an initial wet reaction. The humidity reactions of *Ptinus tectus*

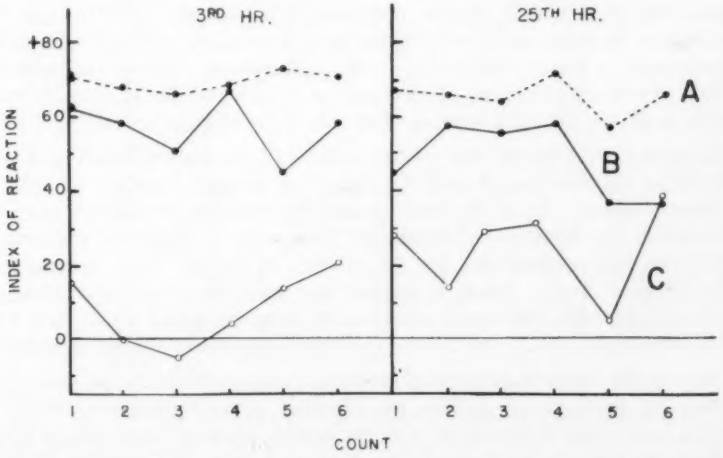

Fig. 6. The effect of humidity alternatives of 100 and 75 R.H. on the light reaction. Curve A, wet side in light; curve B, control; curve C, dry side in light. Counts one, two, three, four, five, and six were made respectively after five, 15, 30, 45, 50, and 60 minutes.

(Bentley, 1944), *Tribolium confusum* (Willis and Roth, 1950) and *T. castaneum* (Roth and Willis, 1951) were at first dry, but became wet upon prolonged (2-10 days) desiccation. No such reversal was found with *S. granarius* since mortality began at low humidities after approximately 52 hours. However, beetles conditioned at 100 R. H. gave an initial dry reaction which became wet after several hours. This difference in humidity reaction and longevity at low humidity may be indicative of the normal environment and moisture requirements of these species. *S. granarius* can develop faster at higher humidities; 63 days at 50 R. H. compared with 49 days at 80 R. H., and the rate of oviposition increases with humidity and is maximal at 100 R. H. (Richards, 1947). The other three species live in flour and optimal humidities are lower. *Ptinus tectus* breeds best at 70 R. H. (Bentley, 1944) and *Tribolium confusum* can complete its development in wheat at 6.5 per cent water content (Fraenkel and Blewit in Willis and Roth, 1950).

The physiological state of an animal during experimentation may greatly influence its humidity reactions (Thomson, 1938, Lees, 1948, Perttunen, 1953, and Bursell, 1957). The effect of severe experimental conditioning usually tends to reverse the moisture reaction, e.g., an insect conditioned at 0 R.H. will give a wet reaction. Conditioning also influences the activity and moisture-discriminating abilities of *S. granarius*. Beetles conditioned at 100 R. H. were much more sluggish than those conditioned at 0 R. H. and showed a strong tendency to aggregate. The length of time an aggregation persisted depended on the specific humidity values; the lower the humidity the quicker the aggregation dispersed. Beetles were less sensitive to differences in humidity alternatives especially in the drier range when conditioned at 100 R.H., but after a time they could discriminate almost as well as those conditioned at 0 R. H.

The moisture reactions of *S. granarius* and the effect of conditioning on them may be of some significance to the survival of the species. Since *S. granarius* develops faster, lives longer, and is more fecund at higher humidities, movement towards more optimal higher humidities would be beneficial. However. after an infestation has become established, the moisture content of wheat increases, and may almost double (Agrawal, Christensen, and Hodson, 1957). This moisture increase, along with other factors, produces suboptimal conditions and movement to lower humidities would be beneficial. Given the appropriate humidity alternatives, beetles conditioned at 0 and 100 R. H. would react to moisture as above, i.e., in a manner that would benefit the species.

Richards (1951) found that when a culture of beetles was sifted or disturbed almost all of the beetles avoided the light, but a small number of individuals were photopositive. From the latter group, he was able to isolate a race which went towards the light *when disturbed*. However, if disturbed photonegative beetles were left undisturbed for 30 minutes or longer, they became photopositive (Figs. 7 & 8). Thus, it appears that two reactions have taken place: 1, an excited reaction, the initial reaction on being disturbed which was investigated by Richards (1951), and 2, a completely independent normal light reaction.

One of the more fundamental questions arising from the present study is the effect of numbers of animals participating in an experiment. Very little work has been done in this field, and the results reported here merely illustrate the effect numbers can have on one reaction of *S. granarius* (see Fig. 8). Most, if not all, of the work in the humidity preference field has been carried out by arbitrarily selecting some fixed number of animals to be used in an experiment.

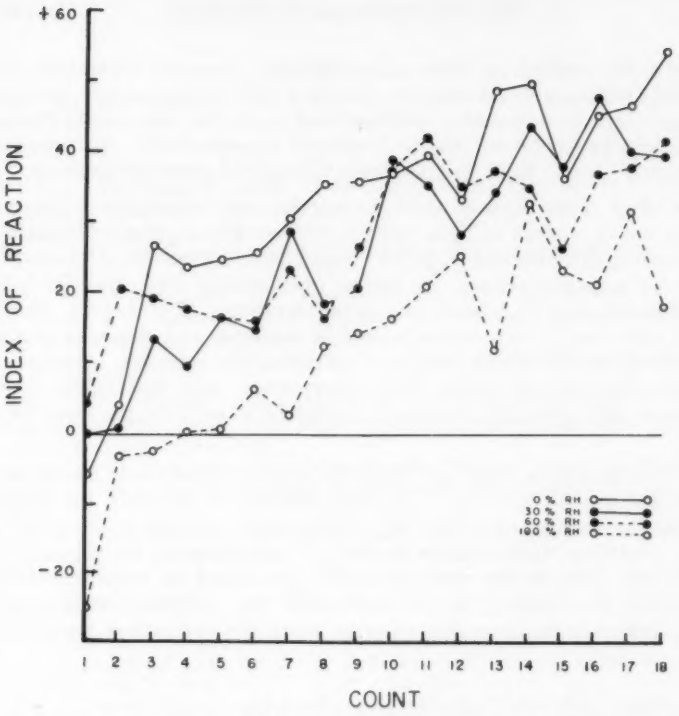

Fig. 7. Effect of relative humidity on the development of the light reaction. Counts one to eight were made at 15-minute intervals, and counts nine to 18 at hourly intervals.

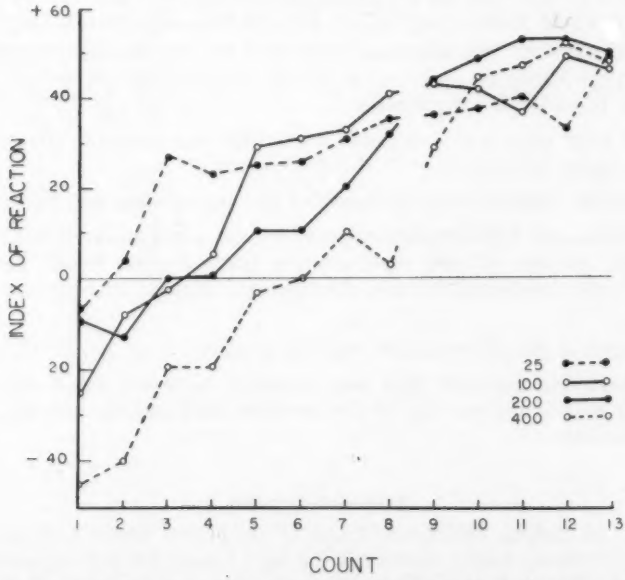

Fig. 8. Effect of group size on the speed of development of the light reaction. Counts one to eight were made at 15-minute intervals; and counts nine to 13 at hourly intervals.

The only study noticed on effect of numbers in a reaction experiment was that of Gauvin (1941), who found that individual field crickets were photopositive but groups were photonegative. Unfortunately, he did not specify the number of insects in a group or the length of time of an experiment. In future experiments of this nature, more consideration should be given to numbers.

This effect of numbers on the light reaction may help confirm the statement that there are two types of light reaction. Since larger groups of beetles maintain themselves in an excited stage for longer periods, they would remain photonegative for a longer period. A similar phenomenon was observed when the beetles were tracked to a point source of humidity. If 10 beetles were in the chamber, only one or two beetles would be attracted and then only for a short while, but all individuals in groups of 25 would be intensely attracted for up to 30 minutes, beyond which time observations were not made. Evidently large groups of *S. granarius* maintain themselves in an excitable state for longer periods.

The interaction of light and humidity of *S. granarius* may be considered a study in strength of stimulus. The light stimulus is probably the stronger of the two and an interaction occurs only under conditions which also give a strong humidity reaction. Only then will there be significantly more beetles on the light-wet side than on the dark-dry side. The effect of varying overall light intensity was not studied, but it was found that complete darkness did not noticably influence the humidity reaction when the alternatives were 30 and 60 R. H.

Summary

1. *S. granarius* reacted to differences in relative humidity. Conditioning at 0 R. H. produced a wet reaction and conditioning at 100 R. H. produced an initial dry reaction which changed to a wet reaction after several hours.

2. The intensity of reaction was influenced by the humidity gradient and position on the humidity scale; the larger the gradient and the wetter the alternatives, the more intense the reaction.

3. Beetles were more active at lower humidities, but remained alive for longer periods at higher humidities.

4. *S. granarius* oriented itself to humidity by hygrokinesis and klinokinesis.

5. *S. granarius* was initially photonegative but became positive if left undisturbed. Smaller groups became photopositive quicker than larger groups, and groups at lower humidities became photopositive quicker than groups at higher humidities.

6. A reversal of the photopositive reaction occurred at 11 to 7.0° C. at 0 R. H.

7. An interaction between light and humidity occurred when the humidity alternatives were at the wet end of the humidity scale and the humidity gradient was 30 per cent.

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Some Factors Influencing the Occurrence and Size of the Midsummer Flight of the European Corn Borer, *Ostrinia nubilalis* (Hbn.) (Lepidoptera: Pyralidae), in Southwestern Ontario[1]

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In southwestern Ontario the European corn borer, *Ostrinia nubilalis* (Hbn.), produces two flights annually. The first flight, beginning in June, consists of moths from larvae that have overwintered. The midsummer, or second, flight begins late in July or early in August, and its moths are the progeny of the first flight. Until about 20 years ago the borer produced only one annual flight and was thought to be univoltine. The change in the seasonal history of the borer in Ontario was described by Wressell (1953) and Miller (1956). The literature describing similar changes in parts of the United States has been reviewed by Lees (1955) and Everett *et al.* (1958). Wressell (1953) summarized light trap collection data of moth flights in the Chatham, Ontario, area for the years 1932 to 1951. The summary includes the percentage of the moths that were from the midsummer flight, and it is evident that the size of this flight varies greatly from year to year. Aside from its intrinsic interest, it would be of some economic value to know what governs the size of the midsummer flight. This is a report of studies undertaken to examine the case, and to relate the findings to the larger problem of why the borer now produces a second flight where formerly it produced only one.

Babcock (1927) found that desiccation of the overwintering larvae delayed emergence in the spring and concluded that effects produced during dormancy led to an increase in univoltinism in the descendants. Prebble (1941) points out that "the delayed spring emergence may have retarded subsequent development to a time at which seasonal changes, *per se*, induced diapause, ..." O'Kane and Lowry (1927) observed that larvae from eggs hatching early in the season might complete development, but those from eggs hatching somewhat later entered diapause. Mutchmor and Beckel (1958, 1959) showed that the occurrence of diapause is governed in part by the photoperiod prevailing during the final larval stage, and suggested that factors influencing the early development of first-generation larvae will determine the proportion of borers completing development and contributing to the production of the second flight.

The causes for the apparent change in voltinism following establishment of the borer in a region are not well understood. The borer is generally believed separable into two strains, the univoltine and the multivoltine. Vance (1939) presented evidence that there are physiological differences between borers with one- and two-generation histories in Ohio, Michigan, and Indiana. Arbuthnot (1944) compared and interbred borers from one- and two-generation areas and, in addition to demonstrating developmental differences, concluded that voltinism is determined genetically. He also found (1949) that the number of generations in various parts of the world is associated with regional differences in rainfall and temperature. The current view on changes in voltinism is stated by Arbuthnot (1949): "The strain best suited to survive in each environment will predominate and may obscure the presence of the less-favoured strain. In order to reach equilibrium, however, both strains must have been present in a region for a sufficient length of time for the environment to have exerted its influence. This process may require considerable time when the less-favoured strain reaches a

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region ahead of the one best-suited to survive in the environment." Following this hypothesis one might say that in southwestern Ontario the univoltine strain was introduced first and became well established. The multivoltine strain, introduced at a later date, proved to be better suited to the environment of the region and, in recent years, has become the dominant strain.

It is the purpose of this paper to present an alternative hypothesis for the apparent change in voltinism of the borer in southwestern Ontario, and for the yearly fluctuations in the size of the midsummer flight. The rationale for the hypothesis may be outlined as follows: Since the induction of diapause is governed by photoperiod, the advent of diapause-inducing conditions will occur at about the same time each year. Borers hatching from eggs laid early in the season will be less likely to enter diapause than those hatching from eggs laid later. Thus, the relative size of the midsummer flight should be determined, at least in part, by the earliness of the first flight. Since the size of the midsummer flight has increased in recent years a corresponding shift to earlier first flights should also have occurred. Spring temperatures should have a major effect on the earliness of the first flight by influencing the rate of post-diapause larval and pupal development. High temperatures will tend to be followed by larger midsummer flights. Thus, a trend to higher spring temperatures might in itself be the cause of the apparent change in voltinism, and yearly variations in that temperature a cause of variation in the size of the midsummer flight.

Materials and Methods

The influence of hatching-date on the occurrence of diapause, and the seasonal change in the environment from diapause-preventing to diapause-inducing, were documented as follows: Groups of multivoltine larvae were placed for rearing in a screened outdoor insectary at intervals through the spring and summer of 1957 and 1958. In 1957 six groups totalling 644 newly-hatched larvae were placed outdoors between May 13 and August 2. In 1958 three groups totalling 91 larvae in the penultimate instar, and six groups totalling 322 newly-hatched larvae, were placed in the insectary between May 14 and August 4 and between June 6 and July 28, respectively. Each larva was in a cotton-stoppered one-dram shell vial containing the modification of Beck's diet (Beck, *et al.* 1949) used previously (Mutchmor and Beckel, 1959). New food was supplied as required. The dates of moults, pupation, or death were recorded for each larva. Temperature was recorded in a nearby standard weather shelter. The larvae were in the shade at all times. Larvae that failed to pupate were placed at 80°F.-85°F. for seven days; they were considered in diapause if they had not pupated before the end of that period.

The influence of temperature on the rate of post-diapause larval development was determined by rearing two replicates of 20 and 25 overwintered larvae at temperatures of 57°F., 65°F., 80°F., and 85°F. These larvae were dissected from corn stalks in mid-March and transferred to the desired temperature immediately. Each larva was over a plug of damp cotton in a cotton-stoppered one-dram shell vial. Dates of pupation and mortality were recorded. Developmental time was taken as the number of days from dissection of the corn to pupation.

Chatham light trap records for the period 1932 to 1957 were used in studying the relationship between the earliness of the first flight and the size of the second. The trap was operated each year except 1943 and 1946. Wressell (1952) has described the trap and its operation. For each year the number of moths captured was plotted cumulatively against the date of capture. From such curves it was generally not difficult to separate the first from the midsummer flight. The

relative size of the midsummer flight was then expressed as the per cent of second flight moths in the total number of moths captured in the season. The date on which 25 per cent of the first flight was completed each year, expressed as "days from June 1 for completion of 25 per cent of the first flight", was used to indicate the earliness of that flight.

Temperature records for Chatham for the period 1921 (when the borer was discovered in Ontario) to 1957 were obtained from the Monthly Record of the Meteorological Division of the Canada Department of Transport, and from its Canada and Dominion Sugar Company, Limited, Chatham, Ontario, Climatological Station Reports. Particular attention was given the records for April, May, and June since temperatures then are likely to influence the rate of post-diapause development and, hence, the earliness of the first flight. Temperature trends from 1921 to 1957 were studied by calculating and plotting the cumulative percentual deviations, of the maximum, mean, and minimum April, May, June, and Spring temperatures, from the respective means for the period 1921-1957. Spring temperatures are defined as the averages of the monthly values for April, May, and June.

Results

1. *Influence of hatching-date and day-length on the occurrence of diapause.*

Groups of borers were reared in the outdoor insectary at intervals during the spring and summer of 1957 and 1958. The 1957 results, in Table I, illustrate the seasonal change in the occurrence of diapause and the importance of hatching-date on its occurrence.

TABLE I

The influence of time of hatch on the subsequent occurrence of diapause in corn borer larvae

Date of hatch	No. of larvae	Mortality (%)	Days to 50% pupation	Diapause (%)
May 13.....	105	93	62	0
June 6.....	146	64	36	0
June 18.....	102	51	35	31
July 8.....	90	65	39	72
July 18.....	100	80	—	100
August 2.....	100	65	—	100

In 1958 similar results were obtained, but the date on which each larva began the final instar was recorded. Since the beginning of that instar is the critical age for induction of diapause (Mutchmor and Beckel, 1959), it was possible to determine the time at which the environment passed from diapause-preventing to diapause-inducing. After entering the final instar during the five-day periods beginning May 15, June 25, 30, July 5, 10, 15, 20, 25, August 4, 9, 14, 19, and 24, the numbers of larvae that entered diapause or pupated (bracketed values) were, respectively, 16 (11), 0 (16), 0 (15), 0 (1), 0 (3), 1 (4), 10 (3), 2 (0), 6 (0), 32 (0), 15 (0), 15 (0), and 19 (0). Despite high mortality that greatly reduced the number of larvae in the experiment, the transition to those entering diapause is well defined. In Fig. 1 the change in the occurrence of diapause is compared with the seasonal change in day-length. From about July 14 to July 25 the percentage of larvae that subsequently entered diapause increased from 0 to 100. Day-length decreased to less than 15 hours in the same period. These results agree with those of laboratory photoperiod studies, in which a similar increase in the occurrence of diapause took place as photoperiod was decreased from 16 to 14 hours (Mutchmor and Beckel, 1959). No major shifts in temperature

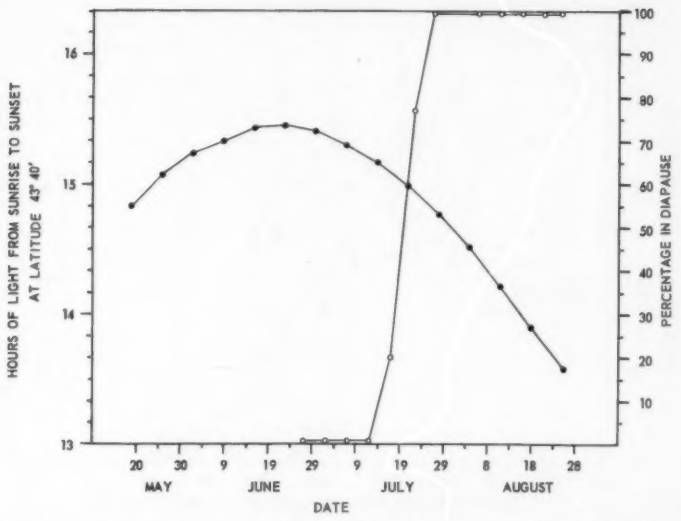

Fig. 1. Changes in day-length and the induction of diapause. Solid circles: Hours from sunrise to sunset at latitude 43° 40'. Open circles: Percentages of larvae that entered diapause after beginning the final instar in the indicated periods.

occurred which could account for the sharp change in the occurrence of diapause in July. Thus, there appears to be an excellent association between day-length in the latter part of July and the change in the incidence of diapause. The induction of diapause in 59 per cent of the borers beginning the final instar in May, before day-length had increased to 15 hours, further supports the relationship.

2. *Relationship between size of midsummer flight and earliness of first flight.*

With day-length as a factor the seasonal transition to an environment inducing diapause should occur at nearly the same time each year. Presumably all larvae will enter diapause except those reaching the final instar before days have shortened to the critical length. Hatching-date, therefore, is a determinant of the number of larvae entering diapause. The earliness of the flight of parent moths should have a similar effect, and thus should be a factor influencing the size of the second flight.

Fig. 2 shows the relationship between the earliness of the first flight and the relative size of the second flight for the period 1932 to 1957. It is evident, despite a wide scatter of points, that early first flights tend to be followed by large midsummer flights. The coefficient of correlation for these data is -0.763, the standard error of estimate $=17.3$. When dates of first moth capture were used to indicate the earliness of the first flight the correlation was, as expected, much poorer ($r= -0.314$).

Since the size of the midsummer flight has increased in recent years it follows that the earliness of the first flight has also increased. This is indicated by the distribution of years associated with the points of Fig. 2.

3. *Spring temperatures and the earliness of the first flight.*

In Fig. 3 cumulative percentual deviations from the respective means for the period 1921 to 1957 have been plotted for the maximum, mean, and minimum

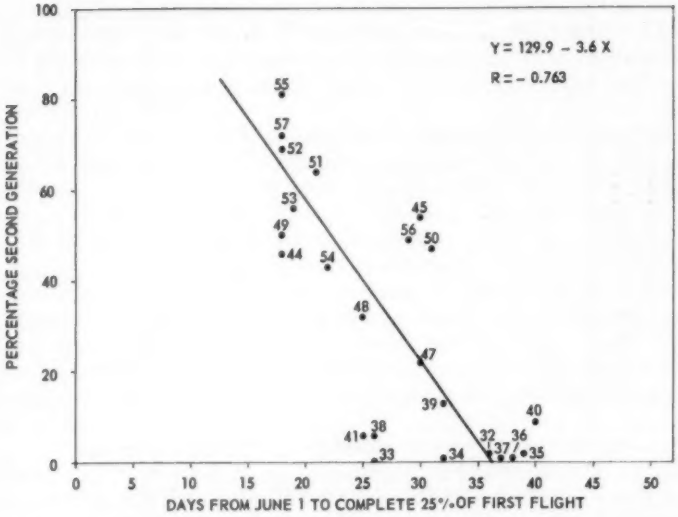

Fig. 2. Relationship between the earliness of the first flight (expressed as the number of days from June 1 to completion of 25 per cent of the flight), and the relative size of the mid-summer flight (expressed as the percentage of second generation moths in the total number of moths captured each year). Numerals with each point indicate the year of the observation. Regression line, $Y = 129.9–3.6X$; coefficient of correlation, –0.763; standard error of estimate $\pm$ 17.3.

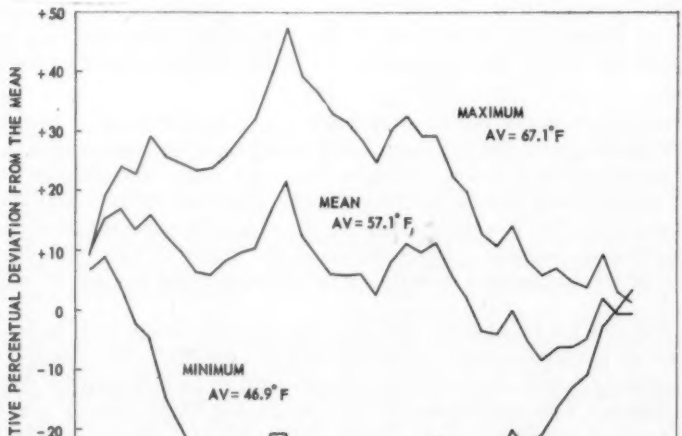

Fig. 3. Trends in spring temperature. Cumulative percentual deviations of the maximum, mean, and minimum temperatures, averaged in each year for April, May, and June, from the respective means (67.1, 57.1, and 46.9°F.) for the period 1921 to 1957.

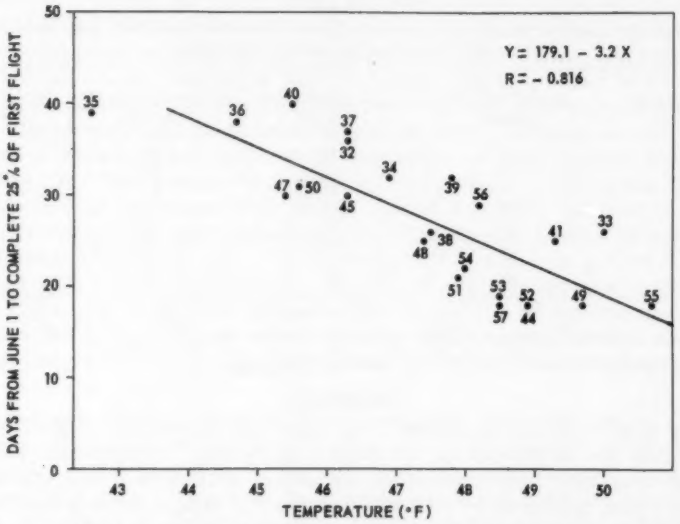

Fig. 4. Relationship between the earliness of the first flight and the mean minimum temperatures averaged for April, May, and June. Numerals with each point indicate the year of the observation. Regression line, Y=179.1-3.2X; coefficient of correlation, -0.816; standard error of estimate, ±4.3.

temperatures averaged for April, May, and June (spring temperatures). Maximum spring temperature has been generally below the average from 1935 to the present. Mean temperature has fluctuated above and below the average, though a slight downtread is indicated. The curve for minimum temperature is broadly U-shaped and represents the pattern for each of the three months. The shape of this curve shows that minimum spring temperature has undergone a general increase in the period 1921 to 1957. From 1921, when the borer was found in Ontario, to about 1938 the minimum temperatures were generally below 46.9°F., the average for the period 1921 to 1957. Since then they have generally been above the average. This corresponds closely to the beginning of the increase in the relative size of the midsummer flight of moths.

Fig. 4 shows that a high degree of correlation ($r = -0.816$; standard error of estimate, ±4.3) exists between the earliness of the first flight and the minimum spring temperatures.

Early first flights tend to follow high minimum spring temperatures. In the period 1932 to 1957 minimum spring temperatures ranging through approximately 8°F., from nearly 43°F. to 51°F., are associated with a range of 22 days in the earliness of the first flight.

Overwintered larvae were placed at various constant temperatures as a means of obtaining information on the magnitude of the effect of small temperature differences, in the thermal range occurring in the spring, on developmental time. The results are summarized in Table II. When replicates were averaged and the reciprocals of developmental time (100/T) plotted against temperature, a straight line was obtained having the equation $Y = -4.93 + 0.106\,X$ where $Y = 100/T$ and X=°F. When Y=0, X=46.4°F. This curve shows that small temperature differences in the low part of the range will have a much greater influence on developmental time than similar differences at higher temperatures. Thus, the

TABLE II
Developmental time of overwintered corn borer larvae dissected from corn stalks in March and reared at various constant temperatures

Temperature (°F.)	Initial No. of larvae	Larval mortality (%)	Larval period (days)	100/Larval period
57	25	36	86	1.16
57	20	20	87	1.15
65	25	92	51	1.96
65	20	55	55	1.82
80	25	44	25	3.94
80	20	45	29	3.45
85	25	23	25	3.95
85	20	45	25	4.03

difference in developmental time between larvae at 52°F. and 56°F. would be 71 days, but between 72°F. and 76°F. only five days.

Discussion

The relative size of the second moth flight and the earliness of the first flight undoubtedly are influenced by a complex of factors. Temperature, moisture, nutrition, and other factors affecting the rate of development and mortality of eggs and larvae produced by first flight moths will influence the proportion and number of larvae completing development before the seasonal change to conditions inducing diapause. That the earliness of the first flight is itself an important factor is indicated both by the degree of correlation ($r = -0.763$) between it and the relative size of the second flight, and as a logical consequence of the seasonal character of diapause induction. Similarly, the earliness of the first flight may be influenced by factors other than temperature. Babcock (1927) found, for example, that dry conditions delayed emergence in the spring. However, the high degree of correlation ($r = -0.816$) between earliness of moth flight and minimum spring temperature suggests a causal relationship. The reasons why changes in minimum, rather than mean or maximum, spring temperatures should have a marked effect on time of emergence are uncertain. The larva spends only a small fraction of its developmental period exposed to minimum or maximum temperatures. Fig. 3 shows that from 1935 below-average maximum temperatures generally offset the above-average minimums, resulting in a near-average mean. The study of developmental rates of overwintered larvae at constant temperatures showed that small differences in temperature in the low thermal range for post-diapause larval development could greatly alter the developmental time, whereas similar differences at higher temperatures had only small effects. Minimum spring temperatures fall in the low thermal range for larval development. Fig. 4 shows that the earliness of the first flight has varied by only 22 days. It seems probable, therefore, that the differences in minimum temperature are adequate to account for the observed annual differences in the earliness of the first flight; this despite the short periods of exposure to such temperatures and, in some years, the opposing influence of maximum temperatures. Before a more specific account can be given of the influence of temperatures on time of emergence, more information is needed concerning the effect of naturally alternating high and low temperatures on post-diapause larval development. As Messenger (1959) points out, the use of results from constant temperature studies in interpreting climatic influences in the field is open to criticism.

If the correlations indicated by this study represent cause-and-effect relationships, then the following interpretation of the changes in the seasonal history of the corn borer can be considered. For about 17 years following the borer's

discovery in Ontario, minimum spring temperatures were generally lower than the 1921-1957 average. The low temperatures, by their effect on the rate of post-diapause larval and pupal development, caused relatively late first moth flights. As a consequence, the progeny of these moths were produced too late to complete development before the onset of diapause-inducing day-lengths in July. Hence, little or no second flight occurred during those years. During the period 1921-1957 the minimum spring temperatures gradually increased, so that from about 1938 they have been above the average for the period. In the years following 1938, the increasing temperature has permitted increasing proportions of the population to emerge early enough to produce progeny capable of completing development without diapause. As a result, the size of the second flight has increased to its present proportions. Annual variations in the relative size of the second flight may result from differences in the earliness of the first flight. The change in the seasonal history of the borer in southwestern Ontario can thus be attributed to the effects of a changing climate on multivoltine corn borers.

Summary

Day-length appears to be a factor governing the induction of diapause. The onset of day-lengths sufficiently short to induce diapause is in the latter half of July. Hatching-date in the spring, by limiting the time available for development, is a factor determining whether larvae enter the final instar before or after the advent of diapause-inducing conditions and, therefore, whether they enter diapause or contribute to production of the midsummer flight. The earliness of the first (spring) flight should have a similar effect; analysis of light trap records revealed a moderately high degree of correlation ($r = -0.763$) between the earliness of the first flight and the size of the midsummer flight. A high degree of correlation ($r = -0.816$) was found between minimum spring temperatures and the earliness of the first flight. Minimum spring temperatures at Chatham, Ontario, have undergone a general increase in the period 1921 to 1957, and since 1938 have been generally above the average for the period. It is suggested that the borer's change from the one- to the two-generation habit in Ontario resulted from climatic changes rather than from a reversal of dominance of voltine strains.

Acknowledgments

The author wishes to thank Mr. G. F. Manson for his invaluable advice and constant interest during the course of this study, and Mr. H. B. Wressell who has operated the light trap and assembled the capture data since 1941.

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(Received June 16, 1959)

Revisional Notes on the Provancher Types of Ichneumoninae (Hymenoptera)

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During November, 1958, I studied the Provancher types of Ichneumoninae in the Provincial Museum of Quebec. My work was very much facilitated by the kind assistance of subdirector Noel-M. Comeau, who has arranged the once badly neglected historical specimens in a most exemplary way, securing them against any further damage as well as saving the time of the visiting specialist. I have only to regret that the revision of all Provancher types, which Mr. Comeau has accomplished by many years' endeavour, is not yet published and therefore not available yet to scientific workers.

As a result of my studies I propose the following taxonomic changes in the arrangement given by Townes (1951).

New Synonyms

Ichneumon deliratorius L., 1761, Fauna Suec., p. 401; ♂.
Ichneumon varipes Prov., 1875, Nat. canad. 7: 22, 50 (preocc.); ♂.
Ichneumon signatipes Prov., 1875, Nat. canad. 7: 22, 52 (preocc.); ♀.
Ichneumon cinctitarsis Prov., (nom. nov. for *varipes*), 1877, Nat. canad. 9: 7; ♂.
Ichneumon stygicus Cress. (nom. nov. for *signatipes*), Amer. Ent. Soc. Trans. 6: 151. 1877.

Barichneumon anator F., 1804, Entom. system. II 1793 p. 169 n. 149.
Ichneumon helvipes Cress., 1867, Trans. Amer. Ent. Soc. 1: 297; ♂, ♀.
Phygadeuon niger Prov., 1876, Nat. canad. 8: 317; ♀.
Phygadeuon electus Prov., 1886, Addit. Corr. Fauna Ent. Canada, Hym., p. 51; ♂.

Ichneumon trizonatus Prov., 1877, Nat. canad. 9: 8; ♂.
Ichneumon ctenuchae Cushm., 1933, Proc. U.S. Nat. Mus. 82: 3; ♀.

The association of the sexes was confirmed by material in the Canadian National Collection reared from *Ctenucha virginica* Charp.

Exephanes terminalis Prov., 1874, Nat. canad. 6: 284; ♀.
Ichneumon pomilius Prov., 1877, Nat. canad. 9: 9; ♂.

The sexes were associated on the basis of morphological characters but also of many observations in the field: of similarities in ecology, distribution, and frequency, especially in Maine during 1956, when the species was exceptionally common.

Species or Subspecies Resurrected from Synonymy

Platylabus rifipes Prov.
Phygadeuon rufipes Prov., 1875, Nat. canad. 7: 181, 183; ♀.

Not identical with *lineolatus* Prov. but a good species differing by the:

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a) distinctly projecting teeth of the propodeum; b) considerably denser and stronger puncturation of the mesonotum; c) stouter tarsi; d) distinctly infuscated lobes of mesonotum.

In the Canadian National Collection this species is represented by one specimen from British Columbia, which agrees exactly with the type specimen from Quebec; and by two specimens from Alaska, which differ subspecifically by lack of the white annulus of the flagellum (*Pl. rufipes consors* Cress.).

Cratichneumon unifasciatorius vancouveriensis Prov.

Ichneumon vancouveriensis Prov., 1885, Canad. Ent. 17: 114; ♂.

The type specimen as well as eight other specimens from Vancouver Island and the mainland of British Columbia in the Canadian National Collection lack the white annulus of the flagellum typical of the male of this species in Eastern Canada. Furthermore, all these specimens are considerably less white marked than the eastern populations. Therefore the Provancher name may not be considered as a synonym but should be applied to the western subspecies.

Aoplus ruficeps vagans Prov.

Ichneumon vagans Prov., 1875, Nat. canad. 7: 22, 51; ♂.

The occurrence of females of *Aoplus ruficeps* (Grav.) in the Nearctic region was recorded by Heinrich, Canadian Ent. 88: 648-649. The males of *I. vagans* Prov. were associated with the females of *A. ruficeps* (Grav.) by two rearings of each sex from *Macaria* sp. in New Brunswick. These rearings also confirmed the correctness of the association of the sexes of *A. ruficeps ruficeps* (Grav.) as published by Heinrich (Mitt. X Munch. Ent. Ges. 35-39: 6, 1949). The color of Nearctic females is within the variation of European populations, whereas American males differ from European by having dark brown or even black hind femora. On account of this slight, but evidently constant, color difference, the Nearctic population may be considered subspecifically different from the European and the Provancher name may be retained for it.

Cyclolabus impressus Prov.

Phygadeuon impressus Prov., 1874, Nat. canad. 6: 281; ♀.

Ichneumon erythropygus Prov., 1875, Nat. canad. 7: 24, 79; "♀" = ♂.

Ectopilus impressus Townes, 1951, Hym. of Am. North of Mexico p. 281; ♀.

In consideration of the pronounced gastrocoeli with a relatively narrow interval this species is better placed in the genus *Cyclolabus* Heinr. than in *Ectopius* Wesm., the latter being especially characterized by the obsolete gastrocoeli.

The type of *I. erythropygus* Prov. is a male, not a female as described by Provancher and quoted by Townes.

Cyclolabus signatus Prov.

Phygadeuon signatus Prov., 1874, Nat. canad. 6: 282; ♀.

Platylabus signatus Townes, 1951, Hym. of Am. North of Mexico, p. 281; ♀.

In this small species the spiracles of the propodeum are not exactly circular but very shortly oval. In this character it stands between *Platylabus* Wesm. and *Cyclolabus* Heinr. However, the very small size of the spiracles, and especially, the strongly abbreviated propodeum give distinct preference to placement in the latter genus

Asthenolabus scutellatus Prov.

Ischnus scutellatus Prov., 1875, Nat. canad. 7: 111; ♂.

Platylabus scutellatus Townes, 1951, Hym. of Am. North of Mexico, p. 281; ♂.

This species obviously belongs in the genus *Asthenolabus* Heinr., which was erected as a new name for the genus *Stenolabus* Heinr. (preocc.) in the Bonn. Zool. Beitr. 2: 240. 1951.

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A New Subfamily, Macroseiinae Nov., of the Family Phytoseiidae (Acarina: Gamasina)

By D. A. CHANT[1], H. A. DENMARK[2], AND E. W. BAKER[3]

Baker and Wharton (1952) elevated the Phytoseiidae, formerly a subfamily in the Laelaptidae, to family rank and included two subfamilies: the Phytoseiinae and the Podocininae. Evans (1957) subsequently elevated the latter to family rank also, leaving only the subfamily Phytoseiinae in the Phytoseiidae.

Both Evans (1958) and Chant (in press) characterized the Phytoseiidae as having a two-tined palpal claw, a single dorsal shield in the adult, not more than 21 pairs of setae on the dorsal shield, and a ventrianal shield, or remnant thereof, in the adults of both sexes. One of the present authors (H.A.D.) recently collected specimens of a mite that has this combination of characters except that the dorsal shield of the adults is divided into two sub-equal parts instead of being single. Most of the features of this mite indicate that it cannot reasonably be separated from the Phytoseiidae and that the presence of two dorsal shields justifies the erection of a new subfamily, described below.

Macroseiinae, new subfamily

Mesostigmatid mites with palpal claw two-tined, dorsal shield sub-divided into anterior and posterior shields and with not more than 21 pairs of setae. Females with genital shield truncate, longer than wide, with anterior margin folded, and with not more than a single pair of setae. All legs with claws. Metasternal plates small or absent. Peritremal, parapodal, and metapodal plates separate. Both sexes with separate ventrianal shields. Male with spermatodactyl on chelicera, genital orifice anterior to sternal shield, sterniti-genital shield separated from ventrianal shield, and leg II unarmed. Type genus *Macroseius* gen. nov.

Macroseius, new genus

Female.—Large mites, about 575 μ long. Dorsal shield subdivided into anterior and posterior shields. Seta S_1 on anterior shield, S_2 on interscutal membrane near posterior margin of anterior dorsal shield. Seven pairs of dorsal (D) setae; D_1 to D_4 on anterior shield, D_5 to D_7 on posterior shield. Setae L_3, L_4, L_6, L_7, L_9, and M_2 long, thick. Ventrianal shield with one pair of preanal setae. Sternal shield with three pairs of setae. Stigma and posterior end of peritreme swollen, bulbous. Legs, especially I and IV, very long, all with claws, and sparsely clothed with setae; legs III and IV with long macrosetae.

Male.—Chelicera with spermatodactyl. Legs with macrosetae. Setae S_1 and S_2 on anterior dorsal shield. Ventrianal shield fragmented, with five pairs of preanal setae.

Type species *Macroseius biscutatus*, new species.

Macroseius biscutatus, new species

Female.—Length: D_1 to D_7 575 μ; anterior dorsal shield 290 μ; posterior dorsal shield 265 μ. Width of posterior dorsal shield 365 μ. Dorsum covered with two sub-equal shields, anterior and posterior (Fig. 1), with dividing suture between setae D_4 and D_5. Anterior shield smooth and with 10 pairs of setae, four in dorsal, one in median, and four in lateral rows. Seta S_1 on anterior shield. Setae L_2, L_4, S_1 long, thick, smooth. Setae D_2, D_3, D_4, and M_1 minute. Setae L_1 slightly longer than L_2.

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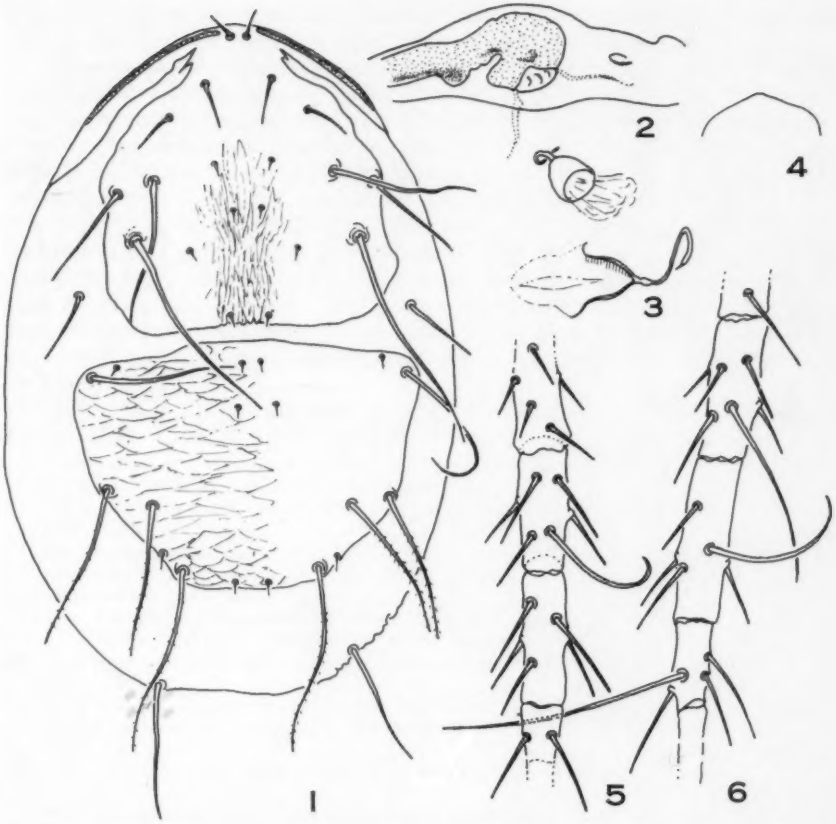
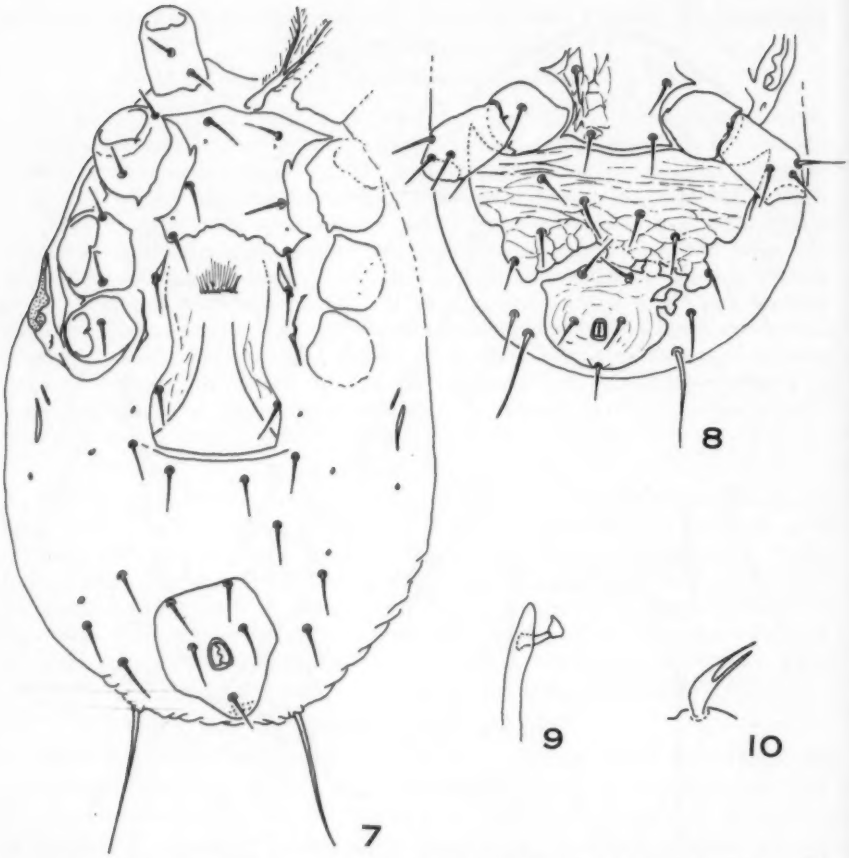


Figs. 1-6. *Macroseius biscutatus* sp.n. 1, female, dorsal surface; 2, peritreme; 3, coxal glands; 4, tectum; 5, leg III; 6, leg IV.

Posterior dorsal shield slightly imbricate, with nine pairs of setae, five in lateral, three in dorsal, and one in median rows. Setae L_6, L_7, L_9, M_2 long, thick, slightly serrated. Setae L_5, D_5, D_6, D_7, L_8 minute. Setae L_3, L_4, L_6, L_7, L_9, and M_2 on slight tubercles.

Seta S_2 on interscutal membrane. Peritreme extended anteriorly to D_1. Anterior end of peritremal plate fused with anterior dorsal shield; posterior end of peritreme and stigma swollen, bilobed, bulbous (Fig. 2). Trachea sclerotized, slightly visible through body wall. Peritremal plate fused posteriorly to exopodal plate, curving around coxa IV. Coxal gland with sinuous duct, bell shaped (Fig. 3). Sternal shield of distinctive shape (Fig. 7), with three pairs of setae. Metasternal plates elongate, each with a seta. Genital shield truncate posteriorly, longer than wide, with a single pair of setae. Two pairs of metapodal plates. Ventrianal shield approximately triangular, 150 μ long, 125 μ wide at anus, with one pair of preanal setae. Six pairs of setae and four small platelets on membrane surrounding ventrianal shield. Seta VL_1 long.

Hypostome normal for family, rostral setae slender. Fixed digit of chelicera with 12 to 15 small teeth and pilis dentilis; movable digit with two or three large



Figs. 7-10. *Macroseius biscutatus* sp.n. 7, female, ventral surface; 8, male, ventral surface; 9, spermatodactyl; 10, palpal claw.

teeth. Tectum smooth (Fig. 4). Palpal claw two-tined (Fig. 10). Legs long: I, 850 μ; II, 720 μ; III, 770 μ; IV, 1020 μ. Legs III (genu) and IV (femur, genu, tibia, and basitarsus) with long macrosetae (Figs. 5, 6).

Male.—Length 550 μ; width 300 μ. Dorsum as in female except seta S_2 on anterior dorsal shield instead of interscutal membrane. Ventrianal shield separated from sterniti-genital shield, fragmented, with five pairs of preanal setae (Fig. 8). Two pairs of setae on membrane surrounding ventrianal shield. Chelicera with spur shaped spermatodactyl (Fig. 9). Legs with macrosetae as in female. Leg II unarmed.

Type Series.—The holotype female, 12 other females, a deutonymph, and two males all collected on *Sarracenia* sp. in Alachua Co., Florida, on June 23, 1958, by Mr. H. A. Denmark, and four females and a male collected on *Sarracenia* sp. in Putnam Co., Florida, on June 3, 1958, by Mr. R. E. Woodruff. The holotype and male allotype are in the United States National Museum, Washington, D.C. Paratypes are in the Canadian National Collection (No. ....) at the Belleville Institute, and the British Museum (Natural History), London, England.

This mite appears to be associated with the frass of a noctuid, *Exyra semicrocea* (Gn.), that feeds on the inside plant tissue of the pitcher plant, *Sarracenia* sp.

Remarks.—It is noteworthy that the suture between the anterior and posterior dorsal shields of *Macroseius biscutatus* is in the usual position for the Parasitoidea i.e., immediately behind the most posterior pair of dorsal (D) setae that comprise the so-called dorsal hexagonal area. Moreover, seta S_2 is associated with the anterior shield and it can be concluded that in the Phytoseiidae the setae of the dorsal posterior interscutal membrane, the marginal series, are absent.

The existence of this dorsally biscutate form further shows that the Phytoseiidae are close to the Digamasellidae as well as to the Aceosejidae. The new form, however, shows a closer affinity to the Phytoseiidae in most characters than to these other families. The absence of armature from leg II in the male and the pattern and number of the setae on the dorsum separate it from the Digamasellidae and its separation from the Aceosejidae follows the lines established by Evans (1958).

Both Evans (1958) and Baker *et al* (1958) gave keys to the families of the Parasitoidea. Couplet 7 of Evans (p. 216) should be amended as follows:

7. Dorsal shield in both sexes with less than 21 pairs of setae; usually no addition of setae on dorsal shield (or shields) after protonymph stage; female with a truncated genital shield and a ventrianal shield; male with sterniti-genital shield separated from ventri-anal shield ..... Phytoseiidae
Dorsal shield with more than 23 pairs of setae except in specialized parasitic forms; setae added to the dorsal shield (or shields) in the deutonymph stage; female with ventrianal or anal shield 8
(i.e., Laelaptidae, Digamasellidae, Aceosejidae, and Eviphididae).

Couplets 37 and 38 of Baker *et al* (p. 28) should be amended as follows:

37. With more than 21 pairs of dorsal setae; ventral and anal plates contiguous or not 38
With less than 21 pairs of dorsal setae; ventral and anal plates contiguous. Predators, usually found on shrubs and trees, or in some cases, fungus or plant feeders ..... Family Phytoseiidae

38. With two sub-equal dorsal plates. Free living or associated with insects ..... Family Digamasellidae
With dorsal shield entire. Predators, usually found on low lying plants or in stored food products ..... Family Aceosejidae

Summary

A new subfamily of mites, the Macroseiinae, of the family Phytoseiidae is described. Both sexes are characterized by having the dorsal shield subdivided into anterior and posterior shields in addition to the usual phytoseiid characters. *Macroseius biscutatus* sp.n., the only known species in the subfamily, was collected from the pitcher plant, *Sarracenia* sp., in Florida and was associated with the frass of a noctuid.

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Note on Feeding Ranges of Six Species of Predaceous Mites (Acarina: Phytoseiidae) in the Laboratory[1]

By H. J. HERBERT[2]

In the laboratory, females of *Typhlodromus tiliae* Oudms., *T.* (*N.*) *rhenanus* Oudms., *T. finlandicus* Oudms., *T. fallacis* (Garm.), *T. corticis* Herb., and *Phytoseius macropilis* (Oudms.) were given various stages of the phytophagous mites *Panonychus ulmi* (Koch), *Bryobia arborea* M. & A., and *Tetranychus telarius* (L.), and *Vasates schlechtendali* (Nal.) to determine their ranges of feeding. The influence of these prey species on growth of phytoseiids and their ability to oviposit was not determined.

Each predaceous species and stage of prey was placed in an individual capsule at 70 ± 2°F. for 24 hours. Each test was replicated ten times. If the mites had fed during this time, coloured photographs were taken by Mr. F. T. Lord of Kentville laboratory, where they are on file.

T. tiliae fed on all stages of the phytophagous mites tested, namely: overwintered and summer eggs, larvae, green nymphs and adults of *P. ulmi* and *B. arborea;* eggs, nymphs and adults of *T. telarius;* and adults of *V. schlechtendali. T. finlandicus* fed on all stages of the phytophagous mites excepting the overwintered eggs of *P. ulmi* and *B. arborea.* Similarly *T.* (*N.*) *rhenanus* and *P. macropilis* did not feed on these overwintered eggs nor the adults of *T. telarius. T. corticis* fed on all stages of *P. ulmi, B. arborea* and *V. schlechtendali* but only on the eggs of *T. telarius. T. fallacis* fed only on the three stages of *T. telarius.* Detailed results are shown in Table I.

TABLE I.

Ranges of feeding of six species of predaceous mites on various stages of four species of phytophagous mites in the laboratory (X, eaten; 0, not eaten).

Phytophagous species and stage	Phytoseiids					
	T. tiliae	*T.* (*N.*) *rhenanus*	*T. finlandicus*	*P. macropilis*	*T. fallacis*	*T. corticis*
Panonychus ulmi						
Overwintered eggs	x	0	0	0	0	x
Summer eggs	x	x	x	x	0	x
Larvae	x	x	x	x	0	x
Green nymphs	x	x	x	x	0	x
Adults	x	x	x	x	0	x
Bryobia arborea						
Overwintered eggs	x	0	0	0	0	x
Summer eggs	x	x	x	x	0	x
Green nymphs	x	x	x	x	0	x
Adults	x	x	x	x	0	x
Tetranychus telarius						
Eggs	x	x	x	x	x	x
Nymphs	x	x	x	x	x	0
Adults	x	0	x	0	x	0
Vasates schlechtendali						
Adults	x	x	x	x	0	x

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Note on the Effect of Spring Flooding on a Population of Wireworms (Coleoptera: Elateridae)[1]

By C. J. S. Fox[2]

Old grassland in Nova Scotia frequently harbours comparatively high populations of wireworms. One such field near Hall's Harbour, Kings County, was found to be mainly infested with the wheat wireworm, *Agriotes mancus* (Say), with *Hypolithus abbreviatus* (Say), *Dalopius pallidus* Brown, and *Ctenicera cylindriformis* (Herbst) forming three, one, and 0.5 per cent of the total population respectively. During 1953-58, for various reasons, a total of 1,216 samples of soil each six by six by eight inches deep with adhering sod were taken from this field. The samples were sifted through ¼-inch mesh screen and the number of wireworms found in each was recorded. The number taken from an area flooded by melted snow and rain for at least three weeks each spring was compared with the number from the surrounding unflooded area. It was found that the average number per square foot in the flooded area was 11.8 and that in the unflooded was 9.2; the difference is significant at the one per cent level of probability. Rather scant records showed that carabid larvae were less numerous in the flooded area and it may be possible that a reduced number of these predators permits a greater survival of wireworms.

The flooding of fields has been considered as a possible control for wireworms in California but Campbell and Stone (1938) concluded that flooding, even for long periods, is relatively ineffective in causing mortality to the sugar beet wireworm, *Limonius californicus* (Mann), unless the soil temperature is 70° F. or above. The literature apparently contains no record of the effect of spring flooding on eastern North American species in cultivated or grass fields. However, MacLeod and Rawlins (1935) counted *A. mancus* (Say) and *H. abbreviatus* (Say) in the high and low areas of potato fields and found injuries to the tubers more prevalent in the lower than in the higher, regardless of the species causing the damage. This and the present evidence indicates that low, moist ground is either more attractive to ovipositing females or permits a greater survival of larvae than higher, drier ground. It also shows that prolonged early spring flooding is not harmful to a population of these species of wireworms, but, on the contrary, favours an increase in their numbers.

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Note on a Cycloptic Specimen of *Lamachus* sp. (Hymenoptera: Ichneumonidae)

By THELMA FINLAYSON[1]

An abnormal adult male of *Lamachus* sp., with a single eye, was reared in the summer of 1939 at Belleville, Ont., from a second-generation cocoon of the spruce sawfly, *Diprion polytomum* (Htg.), collected at Milicin, Czechoslovakia, in September, 1938. The eye (Figs. 1 and 2) occupies the normal position on either side of the head but is continuous over the vertex and extends anteriorly to the antennal sutures. The bases of the antennae are closer together than, and arise from the head in a position slightly ventral to, normal. There are no ocelli present. The head is about three-quarters the length and five-eighths the width of that of an average normal specimen, and gives the appearance of being globular in shape. The other appendages of the head appear normal in shape and position.

This cycloptic condition appears to be rare in insects. It has been recorded in the honey-bee, *Apis mellifera* L., by Dittrich (1891), Lotmar (1936), Lucas (1868), and Stannius (1835). A review of other abnormalities of the eyes and antennae of insects was given by Banerjee and Kevan (1959).

Summary

A specimen of a species of *Lamachus* with the compound eyes confluent over the vertex and without ocelli is described and illustrated.

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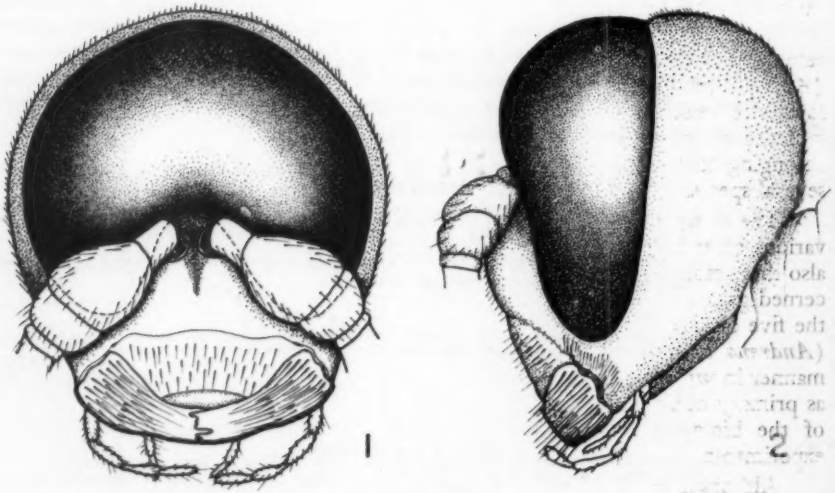

Figs. 1-2. Head of *Lamachus* sp. showing cycloptic eye (darker stippling): 1, anterodorsal view; 2, lateral view.

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(Received September 9, 1959)

Book Reviews

thology of some *Ranunculus* Insects with Emphasis on Competition for Pollen, by E. G. Linsley and J. W. MacSwain, Univ. of Calif. Pubs. in Entom., Vol. 16, No. 1, pp. 1-46, pls. 1-9, 6 figures in text. University of California Press, Apr. 29, 1959. Price $1.00.

This paper reports the results of a study of some insect competitors for the pollen of *Ranunculus californicus* in coastal central California. The work was done in the Berkeley region, at certain carefully selected bee nesting sites in which the dominant flowering plant during the nesting season is *R. californicus*. Observations were made on the behaviour of individual bees in nest construction, flower visits, mating, etc., and on the developmental stages of individual bees, their parasites and predators. In addition, population studies were conducted on all the major insect species associated with *Ranunculus* to obtain comparative information on seasonal and diurnal distributions and numbers, sex ratios, and percentages of parasitism. Among the principal species of pollen gathering bees discussed are several species of *Andrena*, *Panurginus melanocephalus*, and certain species of *Halictus* and *Lasioglossum*. The discussion of miscellaneous competitors includes brief accounts of the habits of a sawfly (*Tenthredo pectoralis*), an empid fly (*Rhamphomyia sudigeronis*), three species of Coleoptera (the cerambycids *Cortodera berkeleyensis* and *Brachysomida tumida* and the elaterid (*Agriotes vandykei*), a root-feeding aphid (*Prociphilus bumeliae*), and several species of pentatomid bugs. The account of the parasites, predators, and diseases includes observations on the habits of bees of the genus *Nomada*, conopid flies belonging to the genera *Myopa* and *Zodion*, a stylopid (*Stylops pacifica*), and several species of nematodes, spiders, mites and fungi.

The study established that in the area selected at least 10 species of bees and ous other insects are important competitors for the pollen of *R. californicus;* that among the bees observed five species are oligolectic and in the area con- gather pollen only from this plant species. It was further noted that of oligolectic species of bees four represent closely related pairs of species *rena complexa* and *A. suavis*, and *A. cuneilabris* and *A. purdyi*). The manner in which such species appear adjusted to permit their continued survival mary competitors is given special consideration by the authors in the light biological differences noted in the course of their observations and experiments.

Although this paper is not a lengthy treatise, the diversity of the information it contains, as evidenced by some of the features noted above, suggests that it will prove of interest and value to a wide group of biological workers.

G. Stuart Walley

Insects of Hawaii. Volume 7. Macrolepidoptera. By Elwood C. Zimmerman. 542 pp., 423 figs. University of Hawaii Press, 1958. Price $9.50.

This continuation of Dr. Zimmerman's treatise maintains the scholarly and opulent standard set by the earlier volumes. The Macrolepidoptera comprise 168 Hawaiian species, 130 endemic and 28 introduced. Dr. Zimmerman has brought to the study of these his characteristic energy, originality and organizing ability. The result is a complete reclassification, the bare list of synonymic changes occupying nearly four pages. While Dr. Zimmerman would be the last to pretend that he has solved all problems of classification of Hawaiian Lepidoptera, his research has greatly clarified the geographic and taxonomic relationships of the fauna. He passes just strictures on the superficial nature of earlier classifications; his personal research has shown that most of his own earlier generalizations on Lepidoptera distribution were false because based on the misleading classifications published by supposed authorities. A new tabular analysis based on the revised classification shows that the endemic species of Macrolepidoptera probably stem from a maximum of 20 immigrations. Dr. Zimmerman attempts to trace these to their sources; and in this he may sometimes be thought overoptimistic: *Eupithecia*, for instance, is as well developed in the tropics and the Antipodes as in the Boreal region, to which he ascribes it, and the Hawaiian species do not particularly resemble Boreal ones in facies; *Agrotis* is not exclusively Boreal, being well developed, for instance, in Australia; *Pseudaletia* is represented in the Old World as well as in the New, and *Plusia*, s.l., in the tropics as well as in the Boreal region. Dr. Zimmerman emphasizes that he has made no effort to search out undescribed species; many of these undoubtedly remain for further students to discover. Specialized studies will no doubt also necessitate changes in certain aspects of Dr. Zimmerman's classification; these, however, are the necessary weaknesses of any comprehensive work. What Dr. Zimmerman has done, and done superlatively well, is to put order into the previous chaos of accumulated data, to reveal areas of knowledge and areas of ignorance, and to provide a clear-cut basis for the new research that his volume must necessarily stimulate. In this accomplishment the details of presentation admirably support the excellent basic design: paper, typography and illustrations are all of the highest quality, and the work as a whole bears the imprint of the array of able collaborators who are very fully acknowledged in the Preface. The historical account of the study of Hawaiian Lepidoptera brings a human touch to the matter of the volume, accentuated by four excellent full-page portraits of outstanding students of the fauna of the Islands.

EUGENE MUNROE.

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